35

# THE ECOLOGY AND CONTROL OF *TYPHA CAPENSIS* IN THE WETLANDS OF THE CAPE FLATS, SOUTH AFRICA

by

DEBORAH J. HALL

Thesis presented for the degree of
Doctor of Philosophy
in the Department of Zoology,
University of Cape Town.

March 1993

## DECLARATION

This thesis documents original research
carried out in the Freshwater Research Unit,
Department of Zoology,
University of Cape Town,
between 1987 and 1990, under the supervision
of Prof Bryan Davies (Zoology Department) and
Prof Eugene Moll (Botany Department).

The work presented has not been submitted
for a degree at any other university.

Any assistance I have received is fully
acknowledged.

Deborah J. Hall...

D.J. HALL

..13 March,..1993...

Date

*To Michael*

*who has strengthened my belief*
*in the necessity of this kind of research.*
*His generation will reap the benefits,*
*or bear the consequences,*
*of the way that we manage our environment today.*

# CONTENTS

## ACKNOWLEDGEMENTS

This project was jointly supervised by Profs. Bryan Davies and Eugene Moll. Their guidance is gratefully acknowledged.

Most of the experimental work was performed on rushbeds located within the Rondevlei Bird Sanctuary. My thanks go to the warden, Mr Howard Langley and his staff for help with, and interest in, this study.

Staff of the Muizenburg Parks and Forests Division of the Cape Town City Council, under the supervision of Mr. Le Roux, did the hard work required to clear, cut and burn experimental areas.

Effecto donated and applied the herbicides. This was arranged through Mr Terry Reddek, who's assistance was greatly appreciated.

The work was jointly funded by the Cape Town City Council, Regional Services Council of the Cape through Rondevlei Bird Sanctuary, and the Foundation for Research and Development, CSIR, Pretoria.

My thanks go to Dr Jenny Day for her interest in the project and for her assistance with the formalities associated with being a student, especially while I was working in Oranjemund.

The encouragement of fellow members of the FRU, especially Jenny, Delny and Jackie, kept me going through the long days of wading knee-deep through boggy rushbeds.

Colin paid the bills, did the proof-reading and was general production dogs-body. Thank you.

# ABSTRACT

The Biology and Control of *Typha capensis*
in the wetlands of the Cape Flats, South Africa.

Deborah Jane Hall
PO Box 823, Oranjemund, Namibia
March 1993

*Typha capensis* is indigenous to the Cape, but is thought to be threatening Cape Flats wetlands through invasion and encroachment. This thesis establishes the extent of such encroachment and investigates aspects of the phenology, life-history, growth, production and decomposition of the species in a Cape Flats wetland. The process of invasion by indigenous species rather than by alien species is discussed and the view that wetlands are threatened by mismanagement rather than by encroachment *per se* is examined. Finally, control methods particularly suited to local environmental and economic conditions are evaluated.

*T. capensis* was shown to be typical of invasive plant species and is spreading in some wetlands. Encroachment is usually associated with the stabilisation of seasonal water-level fluctuations and under these conditions stands were spreading at 1.5m $month^{-1}$.

Demographic methods used to measure growth, production and decomposition made it possible to quantify leaf fragmentation and shoot collapse, processes that are generally ignored during decomposition studies. Results showed that the structure of *Typha* stands is related to flood regime, and that flood regime has an important effect on production, litter formation and decomposition.

Physical (cutting and burning) and chemical (herbicide) control methods were evaluated and found to be most successful when they caused both rhizome and shoot death. This was achieved by flooding cut shoots, or by spraying with herbicides during periods of downward translocation.

This study concludes that *Typha* stands can be permanently removed by cutting shoots to below water level, and keeping them flooded for as long as possible (at least 16 weeks). Thereafter, as this method is dependent on managements ability to control water levels, the use of other environmentally sound control methods are discussed. Fire, flooding and draining can also be used to maintain *Typha* stands at an acceptable size, and in their generative state. Re-invasion of *Typha* is likely and long-term control requires that wetlands are managed to inhibit *Typha* growth. To this end it is strongly recommended that summer drawdown is not reduced.

# CHAPTER 1

# GENERAL INTRODUCTION TO THE STUDY

Wetlands are vital components of river catchments. They act as sponges, recharge aquifers, they buffer floods, and they improve water quality by extracting nutrients and filtering out sediments (Taylor & Cunningham, 1983). In addition, they are highly productive and consequently form the basis of the food chains extending beyond their boundaries (Taylor & Cunningham, 1983; Howard-Williams & Thompson, 1985). Wetlands also have the potential for sustained consumptive and non-consumptive utilisation (IUCN, 1980).

For the purpose of this study wetlands are defined as "...areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water, the depth of which does not exceed six metres." (Ramsar Convention Definition, cited in Department Environmental Affairs, 1991). While this definition is very broad, it is useful because it describes many aquatic systems from bogs, fens and marshes to rivers, reservoirs and estuaries and even coral reefs (Gopal *et al.*, 1990). It was selected for this study because it was important that the widest possible variety of wetland environments were examined in order to determine the range of environmental conditions under which reeds and rushes were growing.

The importance of wetlands was only granted international recognition in 1971, when "The Convention on Wetlands of International Importance Especially as Waterfowl Habitat", was launched (Cowan,

1991). This programme is an international effort to ensure wetland conservation by binding signatories to include wetland conservation in national planning, and to promote their sound utilisation.

South Africa was one of the first signatories to the convention, illustrating its commitment to wetland preservation (Pienaar, 1991). Nevertheless, although seven South African wetlands were immediately declared Sites of International Importance (twenty-two years ago) South Africa has only recently formulated a national policy and strategy for their protection (Breen, 1991; Muller, 1992). In the interim, many local wetlands have been subjected to degradation, the result of injudicious development and uncontrolled catchment practices (Walmsley, 1988; Walmsley & Boomker, 1988).

Estimates concerning the extent and rate of wetland degradation in South Africa are confined to studies by Begg (1986, 1987, 1988) and Breen (1991). Begg has shown that over 29 000ha (62%) of the wetland in the White Mfolozi catchment alone have recently been lost, reducing the proportion of the catchment covered by wetland from 5% to 2.1%. In other parts of Natal and Kwazulu, wetlands are disappearing as rapidly: 34% of the wetlands of the Tugela Basin have been lost; the area of Franklin Vlei has been reduced from 2 500 to 1 060ha; and about 90% of reedbeds, papyrus swamps and riverine forests of the Sibaya catchment have been destroyed (Breen, 1991). Damage is generally attributed to overgrazing, sheet erosion or drainage for agricultural, urban and industrial development.

A recent study of the distribution of wetlands in the south-western Cape shows that most wetlands in the region are farm dams (artificial wetlands), but does not estimate wetland loss or degradation (Silberbauer & King, 1991a). In the Cape Peninsula there are only a few pristine wetlands; the remainder are perceived by the general populace to be wastelands (Day, 1987).

Small, seasonal wetlands have mostly been drained and used for housing. Permanent wetland systems are generally larger, more stable, and more fertile than they once were, the result of increased runoff as the surrounding areas were developed and hardened, and because of sewage effluent inflow. This has resulted in a reduction in habitat- and biotic-diversity (Day, 1987; Langley, 1989). In most Cape Flats wetlands, the reduction in habitat diversity is manifest in the development of large, monospecific stands of bulrush (*Typha capensis* (Rohrb.)).

The conservation of South African wetlands depends upon two factors:

1. innovative legislation policies, and
2. guidelines for their protection and management, with particular reference to the manipulation of plant growth.

While legislation for the protection of wetlands is being addressed by the revision of the Water Act (Act 54 of 1956), the Conservation of Agricultural Resources Act (Act 43 of 1983) and the Forest Act (Act 122 of 1984), the development of guidelines for their management requires research in this neglected area.

Prior to the early 1980s, when the first Wetlands Research Programme was launched by the Council for Scientific and Industrial Research (CSIR), little was known about the ecology of local wetlands. Noble & Hemens (1978) stated that "... totally insufficient information is available on them [wetlands] to take even simple decisions on their conservation, utilisation and management or removal ...". Subsequent research has addressed wetland classification (Geldenhuys, 1981; Morant, 1981, 1983) and inventory (Begg, 1987; Howman, 1987; King, 1987; Silberbauer & King, 1991a,b), the utilisation of wetlands for wastewater treatment (Furness, 1983; Little, 1983; Rogers, 1983; Twinch & Ashton, 1983; Rogers *et al.*, 1985), agriculture (Buchan, 1987) and aquaculture (Merron, 1987) and their management and

conservation (Taylor & Cunningham, 1983; Breen & Begg, 1987, 1989; Ramsden, 1987).

Detailed studies on specific wetlands in South Africa and their ecology are limited to an early study on the ecology of *Phragmites australis* (Gordon-Grey & Ward, 1971) and to the role of vegetation in wetlands (Howard-Williams, 1983). The study reported here, part of a second Wetlands Research Programme, was designed to examine the ecology and control of one of the country's most widespread emergent macrophyte species, *Typha capensis*.

The genus *Typha* has received considerable attention in other parts of the world. It is extremely productive, an attribute which enhances the tendency of its species to invade and to encroach in wetlands so becoming "weeds" (*sensu* Mitchell, 1985) (Nelson & Dietz, 1960; Weller, 1975; Linde *et al.*, 1976; Sharma, 1978; Beule, 1979; Murkin & Ward, 1980; Comes & Kelley, 1989; Sharma & Kushwaha, 1990). High productivity also gives them potential as bio-energy crops (Pratt & Andrews, 1980; Garver *et al.*, 1983) and they are considered useful in wastewater purification systems (Kufel, 1978; Marsh & Bark, 1983; Taylor & Crowder, 1983a,b, 1984, 1986; Sale & Orr, 1986; Reddy & Portier, 1987; Dunbabin *et al.*, 1988; Krishnan *et al.*, 1988).

*Typha* spp. have also been extensively used to test population theories relating to the growth, development, demography and physiological integration of clonal plants (Fiala, 1971a,b, 1973, 1978; Szczepanska & Szczepanska 1976a,b; Sharma & Gopal, 1977; White & Sinclair, 1979; Bell & Tomlinson, 1980; Ogden, 1981; Dickerman & Wetzel, 1985; Grace, 1985, 1987, 1988; Grace & Wetzel, 1981a,b,c, 1982a,b; Djebrouni & Huon, 1988; Jordan & Whigham, 1988; Smith *et al.*, 1988; Ulrich & Burton, 1988), and their responses to environmental gradients (Beare & Jedler, 1987; Grace, 1989). Finally, being a common wetland

genus, its role in wetland moisture, energy, nutrient and vegetation dynamics has been studied by, amongst others, McNaughton & Fullem (1970), Mason & Bryant (1975), Howard-Williams (1975a,b), Krolikski (1978), Laing (1980), Neeley & Davis (1985), Hill (1987), Hogg & Wein (1987) and Mallik (1989).

By comparison with other species in the genus, *T. capensis* has received little attention apart from inclusion in ecosystem productivity and distribution studies (O'Callaghan, 1980; Howard-Williams, 1980; Thompson, 1985; Weisser *et al.*, 1987; Boucher, 1988), including its nuisance weed infestations of canals, lakes and dams (Mitchell, 1985). It is, however, recognised as being widely distributed in freshwater wetlands that have relatively stable hydrological regimes, where its rapid spread may cause management problems (Thompson, 1985; Mitchell, 1985).

Weed infestations have become a problem on the Cape Flats, where the "explosive expansion" of *T. capensis* between, and within, wetlands has been difficult to control (Langley, 1987; 1989; Quick, 1989; Thornton & Boddington, 1989). Middlemiss (1974) reported that in 1952 there were fifteen *Typha* plants in the south-eastern corner of Rondevlei. The wetland is now completely surrounded by *T. capensis* which is still encroaching, threatening all open water space (Langley, 1987). Langvlei and Zeekoevlei are similarly threatened by *T. capensis* (Quick, 1989). Apart from reducing the area of open water and therefore altering the nature of the wetland environment, the stands interfere with recreational use (boating, fishing, skiing), they block inflow and outflow channels increasing siltation rates and causing upstream flooding, and *T. capensis* seeds act as skin and respiratory irritants as well as adhering to fibrous materials thereby causing a nuisance to nearby home owners (Quick, 1987; van Warmelo, 1989). In addition, the loss of habitat diversity caused by *T. capensis* encroachment has resulted in an associated

decline in the number of bird species utilising Rondevlei and Zeekoevlei (Langley, 1987). For these reasons, wetland managers, principally the Cape Town City Council, local Municipalities and the Regional Services Council of the Cape, consider *T. capensis* a "weed".

The successful rehabilitation of the Cape Flats wetlands depends partially on the control of *T. capensis*. To achieve this goal information on both the population dynamics and environmental requirements of *the plant,* under local conditions (Johnstone, 1986; Mitchell, 1985), is required. The study reported here was initiated in order to provide this data. The following key questions were posed to meet the study's objective:

1. What is the distribution of *T. capensis* in the south-western Cape area?
2. Which environmental factors promote encroachment by *T. capensis*?
3. Is the perceived status of *T. capensis* as a "weed" well founded?
4. What effect does flood regime have on the phenology, life-history, growth, production and decomposition of *T. capensis*?
5. Which of the control methods used on *Typha* spp. in other parts of the world are most effective under local conditions?
6. Is the *T. capensis* "problem" a "natural occurrence", the result of exogenous or endogenous disturbance; is it related to the management of wetland ecosystems under urban conditions, or is it a combination of both? How is the problem best addressed?

**THESIS STRUCTURE**

The literature dealing with the biology and control of the genus *Typha* is reviewed in chapter 2 of this thesis. Most of the data come from North America, India and Australia, where *Typha* spp. are considered

"weedy".

Chapter 3 addresses the question "Is *T. capensis* a problem to local wetland managers?" It describes the results of a survey conducted on the Cape Flats, the results of which were used to determine whether or not *T. capensis* is really spreading. The data collected were also used to isolate environmental factors that encourage vigorous *T. capensis* growth, promoting encroachment. Residents living close to wetlands in which *T. capensis* was growing were questioned in order to determine their view on the "problem", so that as wide a view point as possible could be considered.

Chapter 4 describes how demographic techniques were used to describe the phenology, population dynamics and productivity of *T. capensis* in Rondevlei, a freshwater marsh (*sensu* van der Toorn *et al.*, 1991) on the Cape Flats. These methods were developed for the study of plant population dynamics and have been extensively used to test plant population theories (e.g. Bazzaz & Harper, 1977; Harper, 1978; Hartnett & Bazzaz, 1983; Sarukhan *et al.*, 1984). They have also been applied to productivity studies (e.g. Tomlinson, 1974; Bernard, 1975; Bernard & MacDonald, 1974; Dickerman & Wetzel, 1985), and their greater resolution has provided insight into turnover, resource allocation, mortality and longevity.

Chapter 4 also examines the effect of hydrological regime, particularly the extent and duration of flooding, on the demography, growth and production of *T. capensis*. Differences in these characteristics in the plants growing in areas with different flood regimes may be considered to be an expression of intraspecific variability, or of the plasticity exhibited by a single biotype in response to varying environmental conditions. The morphological and physiological variability of a species determines the range of conditions over which it can grow and reproduce (Grace & Wetzel, 1981b). In this regard

flood regime is of great interest for it regulates wetland vegetation dynamics (e.g. Keddy & Reznicek, 1986; Shay & Shay, 1986), restricting species to areas within their water-level tolerance range (e.g. Howard-Williams, 1975b; Grace, 1989). Demographic and growth characteristics of stands growing under a seasonally flooded regime are compared to those of stands which are permanently flooded, or which are never flooded.

Traditionally, decomposition studies begin after litter formation, examining mass and/or nutrient loss from dead plant material (e.g. Mason & Bryant, 1975; Hill, 1985; Davis, 1991). This ignores the processes that take place between leaf senescence and leaf abscission and the inclusion of leaves in the litter layer. In Chapter 5 demographic methods used to estimate these neglected aspects of decomposition are described. Decomposition rate and the rate of litter formation by fragmentation and shoot collapse under different flood regimes are quantified in order to gain some understanding of the effect that large-scale *T. capensis* stand death could have on the wetland environment.

Chapter 6 evaluates the effectiveness of *Typha* control methods used in other parts of the world to control the growth and spread of local *T. capensis* stands. Physical methods, involving removal by cutting or burning in conjunction with shading and flooding, were compared to herbicidal treatment. The advantages and disadvantages of these methods are discussed, together with the use of environmental manipulation in the form of flooding or draining.

The effectiveness of control methods, together with information on the population dynamics (Chapter 4) and environmental requirements (Chapter 3) of *T. capensis* are assembled in order to produce management recommendations for Cape Flats wetlands (Chapter 7). These are formulated with a view to manipulating the

"*Typha* problem" in such a way that it could be regarded in a more positive way. It is proposed that the plant could be used to create employment opportunities in the overcrowded, economically depressed Cape Flats, and simultaneously to generate awareness of the importance of wetlands and their conservation.

The study provides an opportunity to examine the question "What causes the spread of plants whose distribution was previously stable?" Put another way, what causes the reversal of plant status from a desirable indigenous species to that of "weed"? These questions parallel those posed when examining the problem of other invasive plant species, and can be addressed by referring to the theories developed to explain why, how and when plants become invasive (Chapter 7).

**REFERENCES**

BAZZAZ, F.A. & HARPER, J.L. 1977. Demographic analysis of the growth of *Linum usitattissmum*. *New Phytol.*, **78**: 193-208.

BEARE, P.A. & JEDLER, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh - the role of salinity intrusion. *Estuaries*, **10**: 165-170.

BEGG, G.W. 1986. *The wetlands of Natal (Part 1). An overview of their extent, role and present status*. Natal Town and Regional Planning Commission Report 68.

BEGG, G.W. 1987. Distribution and status of wetlands in Mfolozi catchment. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

BEGG, G.W. 1988. *The Wetlands of Natal (Part 2). The distribution, extent and status of wetlands in the Mfolozi catchment*. Natal Town and Regional Planning Commission Report 71.

BELL, A.D. & TOMLINSON, P.B. 1980. Adaptive architecture in rhizomatous plants. *Bot. J. Linn. Soc.*, **80**: 125-160.

BERNARD, J.M. 1975. The life-history of shoots of *Carex lacustris*. *Can J. Bot.* **53**: 256-260.

BERNARD, J.M. & MACDONALD, J.G.Jr. 1974. Primary production and life-history of *Carex lacustris*. *Can. J. Bot.* **52**: 17-123.

BEULE, J.D. 1979. *Control and management of cattails in south-eastern Wisconsin wetlands*. Tech. Bull. No. 112, Department of Natural Resources, Madison.

BOUCHER, C. 1988. Wetland vegetation of the fynbos biome. In: *Hydrology and hydrobiology in the fynbos biome*. King, J.M. (ed.). Occasional report No. 26, Foundation for Research and Development, CSIR, Pretoria.

BREEN, C.M. 1991. Wetlands - the will to find a way. *Conserva*, **May/Jun**: 8-11.

BREEN, C.M. & BEGG, G.W. 1987. Wetlands - a valuable natural resource. *Afr. Wildl.*, **41**: 219-221.

BREEN, C.M. & BEGG, G.W. 1989. Conservation status of South African wetlands. In: *Biotic Diversity in Southern Africa: Concepts and Conservation*. Huntley, B.R. (ed.). Oxford Scientific Press, Cape Town.

BUCHAN, A.J.C. 1987. The use of the Pongolo River floodplain grazing resources by domestic stock. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

COMES, R.D. & KELLEY, A.D. 1989. Control of common cattail with post-emergent herbicides. *J. Aquat. Plant Mngmt.*, **27**: 20-23.

COWAN, G. 1991. Wetlands enjoy high priority for protection. *South African Wetlands*, **1**: 4-7.

DAVIS, S.M. 1991. Growth, decomposition, and nutrient retention of *Caldium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat. Bot.*, **40**: 203-224.

DAY, J.A. 1987. Conservation and management of wetlands in the greater Cape Town area. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

DEPARTMENT OF ENVIRONMENTAL AFFAIRS, 1991. The Ramsar Convention. *South African Wetlands*, **1**: 1.

DICKERMAN, J.A. & WETZEL, R.G. 1985. Clonal growth in *Typha latifolia*: Population dynamics and demography of the ramets. *J. Ecol.*, **73**: 535-552.

DJEBROUNI, M. & HUON, A. 1988. Structure and biomass of a *Typha* stand as revealed by multi-dimensional analysis. *Aquat. Bot.*, 39: 331-342.

DUNBABIN, J.S., POKORNY, J. & BOWMER, K.M. 1988. Rhizosphere oxygenation by *Typha domingensis* Pers. in miniature artificial wetland filters used for metal removal from wastewater. *Aquat. Bot.*, **29**: 303-317.

FIALA, K. 1971a. Seasonal changes in the growth of clones of *Typha latifolia* L. in natural conditions. *Folia Geobot. Phytotaxon.*, **6**: 225-270.

FIALA, K. 1971b. Comparison of seasonal changes in the growth of underground organs of *Typha latifolia* and *Typha angustifolia*. *Hidrobiol. (Romania)*, **2**: 235-240.

FIALA, K. 1973. Growth and production of underground organs of *Typha angustifolia* L., *T. latifolia* L. and *Phragmites communis* Trin. *Pol. Arch. Hydrobiol.*, **20**: 59-66.

FIALA, K. 1978. Underground organs of *Typha angustifolia* and *Typha latifolia*: Their growth, propagation and production. *Priroden Pr. Ustavu. Cesk. Akad. Ved. Brne.*, **12**: 1-43.

FURNESS, H.D. 1983. Wetlands as accreting systems: Inorganic sediments. *J. Limnol. Soc. sth. Afr.*, **9**: 90-95.

GARVER, E.G., DUBBE, D.R. & PRATT, D.C. 1983. Adaptability of *Typha* spp. to various wetland soil conditions for bio-energy production. In: *Proceedings of the International Symposium on Peat Utilisation*. Fuchsman, C.H. & Spigarell, S.A. (eds). Bemdji State University Centre for Environmental Studies, Bemdji, USA.

GELDENHUYS, J.N. 1981. Classification of the pans of the western Orange Free State according to vegetation structures, with reference to avifaunal communities. *S. Afr. J. Wildl. Res.*, **12**: 55-62.

GOPAL, B., KVET, J., LOFFLER, H., MASING, V. & PATTEN, B.C. 1990. Definitions and classification. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgensen, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

GORDON-GRAY, K.D. & WARD, C.J. 1971. A contribution to the knowledge of *Phragmites* in South Africa, with particular reference to Natal populations. *S. Afr. J. Bot.*, **37**: 1-30.

GRACE, J.B. 1985. Juvenile vs. adult competitive abilities in plants: Size-dependence in cattails (*Typha*). *Ecology*, **66**: 1630-1638.

GRACE, J.B. 1987. The impact of pre-emption on the zonation of two *Typha* species along lake shores. *Ecol. Monogr.*, **57**: 283-303.

GRACE, J.B. 1988. The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water-level gradient. *Aquat. Bot.*, **31**: 83-92.

GRACE, J.B. 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *Am. J. Bot.*, **76**: 762-768.

GRACE, J.B. & WETZEL, R.G. 1981a. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies of the intensity of competition. *Am. Nat.*, **118**: 463-474.

GRACE, J.B. & WETZEL, R.G. 1981b. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia*: Experimental studies in marshes of different successional maturity. *Ecology*, **62**: 789-801.

GRACE, J.B. & WETZEL, R.G. 1981c. Effect of size and growth rate on vegetative reproduction in *Typha*. *Oecol.*, **50**: 158-161.

GRACE, J.B. & WETZEL, R.G. 1982a. Variations in growth and reproduction within populations of two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Oecol.*, **53**: 258-263.

GRACE, J.B. & WETZEL, R.G. 1982b. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Can. J. Bot.*, **60**: 46-57.

HARPER, J.L. 1978. The demography of plants with clonal growth. In: *Structure and Functioning of Plant Populations*. Freyson, A.H.J. & Wolderdorf, J.W. (eds). North Holland Publishing Company, Amsterdam.

HARTNETT, J.C. & BAZZAZ, F.A. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology*, **64**: 779-788.

HILL, B.H. 1985. The breakdown of macrophytes in a reservoir wetland. *Aquat. Bot.*, **21**: 23-31.

HILL, B.H. 1987. *Typha* production in a Texas pond: Implications for energy and nutrient dynamics in freshwater wetlands. *Aquat. Bot.*, **27**: 385-394.

HOGG, E.H. & WEIN, R.W. 1987. Growth dynamics of floating *Typha* mats: Seasonal translocation and internal deposition of organic material. *Oikos*, **50**: 197-205.

HOWARD-WILLIAMS, C. 1975a. Seasonal and spacial changes in the composition of the aquatic and semi-aquatic vegetation of Lake Chilwa, Malawi. *Vegetatio*, **30**: 33-39.

HOWARD-WILLIAMS, C. 1975b. Vegetation changes in a shallow African lake. Response of the vegetation to a recent dry period. *Hydrobiologia*, **47**: 381-389.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophytes of the coastal wetlands of Maputaland. In: *Studies on the Ecology of Maputaland*. Bruton, M.N. & Cooper, K.H. (eds). Rhodes University and Wildlife Society of South Africa (Natal Branch), Grahamstown.

HOWARD-WILLIAMS, C. 1983. Wetlands and watershed management; the role of aquatic vegetation. *J. Limnol. Soc. sth. Afr.*, **9**: 54-62.

HOWARD-WILLIAMS, C. & THOMPSON, K. 1985. The conservation and management of African wetlands. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, The Hague.

HOWMAN, A. 1987. Can satellites assist in the inventory of wetland areas? In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

IUCN, 1980. *World Conservation Strategy*. IUCN, Gland.

JOHNSTONE, I.M. 1986. Macrophyte management: An integrated perspective. *N.Z. J. Mar. Freshwater Res.*, **20**: 599-6614.

JORDAN, T.E. & WHIGHAM, D.F. 1988. The importance of standing dead shoots of the narrow-leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **29**: 319-328.

KEDDY, P.A. & REZINCEK, A.A. 1986. Great Lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. *J. Great Lakes Res.*, **12**: 25-36.

KING, J.M. 1987. Inventory of south-western Cape wetlands. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

KRISHNAN, S.S., CANCILLA, A. & JERVIS, R.E. 1988. Waste water treatment for heavy metal toxins using plant and hair as adsorbents. *Sci. Total Environ.*, **68**: 267-273.

KROLIKSKI, J. 1978. The transpiration of helophytes. *Ekol. Polska*, **26**: 193-212.

KUFEL, I. 1978. Seasonal changes in Pb, Cu, Mo, and Co in above-ground parts of *Phragmites australis* Trin. ex Steudal and *Typha angustifolia* L. *Bull. Acad. pol. Sci. Nat. Ser. Sci. Biol.*, **26**: 765-770.

LAING, H.E. 1980. Respiration of the leaves of *Nuphar advenum* and *Typha latifolia*. *Am. J. Bot.*, **27**: 583-586.

LANGLEY, C.H. 1987. *Notes on Typha latifolia: A threat to our wetlands*. Unpublished report, Rondevlei Bird Sanctuary, Cape Town.

LANGLEY, C.H. 1989. Problems caused by *Typha*. In: *Typha: Its status, problems, economic benefits and control*. van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

LINDE, A.F., JANSCH, T. & SMITH, D. 1976. *Cattail: The significance of its growth, phenology and carbohydrate storage to its control and management*. Tech. Bull. 94, Department of Natural Resources, Madison.

LITTLE, A.M. 1983. Planning the rational use of wetlands. *J. Limnol. Soc. sth. Afr.*, **9**: 146-148.

MALLIK, A.U. 1989. Small-scale succession toward fen on a floating mat of a *Typha* marsh in Atlantic Canada. *Can. J. Bot.*, **67**: 1309-1316.

MARSH, L.C. & BARK, P.E. 1983. Bio-accumulation of cadmium, lead and zinc in *Typha latifolia*. *Am. J. Bot.*, **76**: 50-55.

MASON, C.F. & BRYANT, R.J. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, **63**: 71-95.

MCNAUGHTON, S.J. & FULLEM. L.W. 1970. Photosynthesis and photorespiration in *Typha latifolia*. *Plant Physiol.*, **45**: 703-707.

MERRON, G.S. 1987. The response and recovery of fish stocks of the Pongolo floodplain during and after a period of prolonged drought. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

MITCHELL, D.S. 1985. African aquatic weeds and their management. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, The Hague.

MORANT, P.D. 1981. *Wetland classification: a review of existing wetland classification systems and their applicability to southern Africa*. MSc Thesis, School of Environmental Science, University of Cape Town, Cape Town.

MORANT, P.D. 1983. Wetland classification: Toward an approach for southern Africa. *J. Limnol. Soc. sth. Afr.*, **9**: 76-84.

MULLER, M. 1992. Actions of working group promised. *South African Wetlands*, **2**: 3.

MURKIN, H.R. & WARD, P. 1980. Early spring cutting to control cattail in a northern marsh. *Wildl. Soc. Bull.*, **8**: 254-256.

NEELEY, R.K. & DAVIS, C.B. 1985. Nitrogen and phosphorus fertilisation of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. 1. Emergent production. *Aquat. Bot.*, **22**: 347-361.

NELSON, N.F. & DIETZ, R.H. 1960. *Cattail control methods in Utah*. Utah State Department of Fish and Game Publication No. 66-2.

NOBLE, R.G. & HEMENS, J. 1978. *Research on inland water ecosystems in South Africa*. South African National Scientific Programmes Occasional Report No. 34, CSIR, Pretoria.

O'CALLAGHAN, M. 1980. *Gross production and seasonal changes in standing stock of four species of swamp plants in Rondevlei Bird Sanctuary*. Unpublished Report, Botany Department, University of Cape Town, Cape Town.

OGDEN, J. 1981. Studies in the population dynamics of *Typha* at Lake Pukepuke. *N.Z. J. Ecol.*, 4: 124-125.

PRATT, D.C. & ANDREWS, N.J. 1980. Cattails (*Typha* spp.) as an energy source. In: *Energy from Biomass and Wastes*. White, J.W., McGrew, W. & Suttor, M.R. (eds). Florida.

RAMSDEN, H.T. 1987. Legal principles and wetland legislation. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

REDDY, K.R. & PORTIER, K.M. 1987. Nitrogen utilisation by *Typha latifolia* L. as affected by temperature and rate of nitrogen application. *Aquat. Bot.*, 27: 127-138.

ROBERTS, J. 1987. *The autocology of Typha spp. in South-Eastern Australia*. PhD Thesis, University of Adelaide, Australia.

ROGERS, F.E.J. 1983. Wetlands as accreting systems: wastewater treatment. *J. Limnol. Soc. sth. Afr.*, 9: 110-116.

ROGERS, F.E.J., ROGERS, K.H. & BUZER, J.S. 1985. *Wetlands for wastewater treatment with special reference to Municipal Wastewaters*. Witwatersrand University Press, Johannesburg.

SALE, P.J. & ORR, P.T. 1986. Gas exchange of *Typha orientalis* Presl. communities in artificial ponds. *Aquat. Bot.*, 23: 309-320.

SARUKHAN, J., MARTINEZ-RAMOS, M. & PINERO, D. 1984. The analysis of demographic variability at the individual level and its population consequences. In: *Perspectives in Plant Population Ecology*. Dirzo, R. & Sarakhan, J. (eds). Sinauer Associated Inc., Sunderland.

SHARMA, K.P. 1978. Effect of cutting on the growth and flowering behaviour of *Typha elephantina* Roxb. *Current Science*, 47: 275-276.

SHARMA, K.P. and GOPAL, B. 1977. Studies on stand structure and primary production in *Typha* species. *Int. J. Ecol. Env. Sci.*, 3: 45-66.

SHARMA, K.P. and KUSHWAHA, S.P.S. 1990. Effect of cutting on above-ground organs of *Typha angustata* Bory et Chaub on its growth and total chlorophyll content. *Aquat. Bot.*, 36: 293-296.

SHAY, J.M. & SHAY, C.T. 1986. Prairie marshes in western Canada, with special reference to the ecology of five emergent macrophytes. *Can. J. Bot.*, 64: 443-454.

SILBERBAUER, M.J. & KING, J.M. 1991a. The distribution of wetlands in the south-western Cape Province, South Africa. *Sth. Afr. J. aquat. Sci.*, 17: 65-81.

SHAY, J.M. & SHAY, C.T. 1986. Prairie marshes in western Canada, with special reference to the ecology of five emergent macrophytes. *Can. J. Bot.*, **64**: 443-454.

SILBERBAUER, M.J. & KING, J.M. 1991a. The distribution of wetlands in the south-western Cape Province, South Africa. *Sth. Afr. J. aquat. Sci.*, **17**: 65-81.

SILBERBAUER, M.J. & KING, J.M. 1991b. Geographical trends in the water chemistry of wetlands in the south-western Cape Province, South Africa. *Sth. Afr. J. aquat. Sci.*, **17**: 82-88.

SMITH, C.S., ADAMS, M.S. & GUSTAFSON, T.D. 1988. The importance of below-ground mineral element stores in cattails (*Typha latifolia* L.). *Aquat. Bot.*, **30**: 343-352.

SZCZEPANSKA, W. & SZCZEPANSKA, A. 1976a. Effect of density on productivity of *Phragmites communis* Trin. and *Typha latifolia* L. *Pol. Arch. Hydrobiol.*, **23**: 391-400.

SZCZEPANSKA, W. & SZCZEPANSKA, A. 1976b. Growth of *Phragmites communis* Trin., *Typha latifolia* L. and *Typha angustifolia* L. in relation to the fertility of the soils. *Pol. Arch. Hydrobiol.*, **23**: 233-248.

TAYLOR, R.H. & CUNNINGHAM, A.B. 1983. The conservation of wetlands. *J. Limnol. Soc. sth. Afr.*, **9**: 141-145.

TAYLOR, G.J. & CROWDER, A.A. 1983a. Uptake and accumulation of heavy metals by *Typha latifolia* in wetlands of the Sudbury, Ontario region. *Am. J. Bot.*, **66**: 63-73.

TAYLOR, G.J. & CROWDER, A.A. 1983b. Uptake and accumulation of copper, nickel and iron by *Typha latifolia* L. grown in a solution culture. *Can. J. Bot.*, **61**: 1825-1830.

TAYLOR, G.J. & CROWDER, A.A. 1984. Copper and nickel tolerance in *Typha latifolia* clones from contaminated and uncontaminated environments. *Can. J. Bot.*, **62**: 1304-1308.

TAYLOR, G.J. & CROWDER, A.A. 1986. Uptake and accumulation of copper, nickel and iron by *Typha latifolia*. *Am. J. Bot.*, **70**: 56-71.

THOMPSON, K. 1985. Emergent plants of permanent and seasonally-flooded wetlands. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, The Hague.

THORNTON, J.A. & BODDINGTON, G. 1989. Problems associated with the bulrush *Typha latifolia* in Cape Town. In: *Typha: Its status, problems, economic benefits and control*. van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

TOMLINSON, P.B. 1974. Vegetative morphology and meristem dependence - the foundation of productivity in seagrass. *Aquacult.*, **4**: 107-130.

TWINCH, A.J. & ASHTON, P.J. 1983. Wetlands as accreting systems: Nutrient cycling in wetlands. *J. Limnol. Soc. sth. Afr.*, **9**: 104-109.

ULRICH, K.E. & BURTON, T.M. 1988. An experimental comparison of the dry matter and nutrient distribution patterns of *Typha latifolia* L., *Typha angustifolia* L., *Sparganium eurycarpum* Engelm. and *Phragmites australis* (Cav.) Trin. ex Steudel. *Aquat. Bot.*, 32: 129-139.

VAN DER TOORN, J., VERHOEVEN, J.T.A. & SIMPSON, R.L. 1990. Freshwater marshes. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgenson, S.E. & Dumont, H. (eds.). SPB Academic Publishing, The Hague.

VAN WARMELO, W. (ed) 1989. *Typha: Its status, problems, economic benefits and control*. Report on the *Typha* Symposium held at Rondevlei Bird Sanctuary, Cape Town, 9 March, 1989.

WALMSLEY, R.D. & BOOMKER, E.A. 1988. *Inventory and classification of wetlands in South Africa*. Proceedings of a workshop. Occasional Report No. 34, Ecosystem Programmes, Foundation for Research Development, CSIR, Pretoria.

WEISSER, P.J., BOSCHOFF, D.N. & VAN EEDEN, S. 1987. Vegetation and vegetation changes at the Mzingazi lake. In: *Proceedings of a symposium on Ecology and Conservation of Wetlands in South Africa*. Walmsley, R.D. & Botten, M.L. (compilers). Occasional Report Series No. 28, Ecosystem Programmes, Foundation for Research and Development, CSIR, Pretoria.

WELLER, M.W. 1975. Studies of cattail in relation to management for marsh wildlife. *Iowa State J. Res.*, **49**: 383-412.

WHITE, J.M. & SINCLAIR, L.R. 1979. Effect of plant spacing on growth and yield of transplanted cattails. *Proc. Soil Crop Sci. Soc. Florida*, **38**: 18-20.

# CHAPTER 2

# THE BIOLOGY AND CONTROL OF *TYPHA*: A LITERATURE REVIEW

## TAXONOMY

Species of the genus *Typha*, commonly called cattails (America), reedmace (Britain and Europe), cumbungi, maranda and yanget (Australia), bulrush (Australia and Africa) or papkuil (South Africa), are members of one of the most widespread aquatic emergent plant groups in the world (Sculthorpe, 1967). They form a monogeneric family, the Typhaceae, characterised as monoecious, rhizomatous, perennial herbs with erect, unbranched stems, linear leaves with long, open sheathing bases and protandrous, spike-like inflorescences (Napper, 1971).

Between eight and fifteen species are recognised worldwide (Napper, 1971; Smith, 1987) but only one, *Typha capensis* (Rohrb.) (syn. *Typha latifolia* L. subsp. *capensis* Rohrb.) is found in the Cape (Smith, 1987). Early taxonomic treatment described two local species, *T. capensis* and *T. australis* (e.g. Adamson & Salter, 1950), but the latter no longer exists as a separate species. Electrophoretic studies suggest that *T. capensis* may be a hybrid, derived from *T. angustifolia* and *T. latifolia*, known as *T.* X *glauca* Godron. (Smith, 1987). Although *T.* X *glauca* is morphologically similar to its parent species, isoelectrofocusing techniques have shown that their pollen protein profiles are distinct (Krattinger *et al.*, 1979).

Napper (1971) describes *T. capensis* as a branching rhizomatous herb with stout, erect 2 to 4m high stems bearing leaves with long sheaths and linear blades. Leaves arise from the base of the shoot in an

alternate manner. Leaf sheaths have rounded or auriculate scarious-margined shoulders which may be purple spotted within. Blades reach 2m in length and are flat above and convex below. Inflorescences are usually contiguous, but they may be separated by as much as 2cm. The male spike is 8 to 15cm long and, when mature, sheds bright primrose-yellow pollen as single grains. The female spikes develop below the male inflorescences and are 12 to 32cm long. When mature, spikes are reddish-brown with carpodia appearing as off-white spots (Napper, 1971). The fruit is a one-seeded follicle with the stigma and hairs of the female flower forming a pappus, which aids in distribution.

## DISTRIBUTION

*Typha* and *Phragmites* are the only emergent hydrophytes with a cosmopolitan distribution (Sculthorpe, 1967). *Typha latifolia* is the most widely distributed species, being found at all altitudes throughout North America, Eurasia, Africa, New Zealand and Australia, and at latitudes between the Arctic circle and 30°S (Smith, 1967; Napper, 1971; Grace & Harrison, 1986). *Typha angustifolia* is less common, and is generally confined to low elevations in North America, Europe and Britain. *Typha domingensis* is found in southern North America, South America, Eurasia, Australia and some parts of Africa, in tropical, subtropical and Mediterranean climates (Smith, 1967; Napper, 1971), while *T. capensis* is confined to northern Africa, South Africa, the Okavango Delta and some high altitude areas in tropical regions (Smith, 1967; Thompson, 1985). *Typha orientalis* is native to the south-west Pacific (Briggs & Johnson, 1968 in Roberts, 1987). *Typha minima* and *T. schuttleworthii* are native to Switzerland (Krattinger *et al.*, 1979). *Typha elephantina* and *T. angustata* are sympatric in India (Sharma, 1978; Sharma & Gopal, 1980).

Within their ranges, these species tend to be

widespread among wetlands and their distribution is enhanced by the development of permanent or fairly stable water bodies such as impoundments, ponds, irrigation systems and roadside canals (Finlayson *et al.*, 1983; Grace & Harrison, 1986). Water supply is probably more important than rainfall in determining their success.

## HABITAT

*Typha* spp. are found growing in almost every type of wetland, from humid coastal to dry continental areas, high to low altitudes and in wetlands with widely differing pH, salinity and nutrient levels (Pratt & Andrews, 1980). They are confined to wet or saturated soils (soil moisture must exceed 8% - Grace, 1985) and shallow water areas, but they are also common in unstable habitats such as roadside ditches, lakes with widely fluctuating water levels and estuaries (Grace & Wetzel, 1981a; Finlayson *et al.*, 1983; Langley, 1987). Most species are associated with basic calcareous soils and, although the salinity tolerance of seedlings is low, rhizome-bearing shoots are found in saline soils (Beare & Jedler, 1987). They are found in a range of substrata, from fine-textured organic muds to coarse gravel, and are tolerant of anoxic sediments (Finlayson *et al.*, 1983; Sale & Wetzel, 1983). Although they sometimes occur in streams and rivers, *Typha* are generally found in areas with little or no water flow (Anderson, 1976; Krasnova, 1988). *Typha* is able to persist for several years in the absence of flooding as it is relatively resistant to drought (Thompson, 1985). *Typha capensis* is an ubiquitous species in the Cape, being found in most shallow-water wetlands, particularly at the inflows to, or outflows from, seeps, pans and lakes (Boucher, 1988).

## COMMUNITIES

*Typha* spp. are usually found in dense monospecific stands. They also occur as scattered individuals or

clumps in mixed vegetation and in marginal areas such as those with wide fluctuations in water level (Finlayson *et al.*, 1983). The *Scirpus-Phragmites-Typha* association is common in many areas (Howard-Williams, 1980; Shay & Shay, 1986). These species are generally separated along the water depth gradient, with *Typha* occupying areas drier than those colonised by *Scirpus*, but wetter than those by *Phragmites*. Water depth usually separates sympatric species; for example, *T. latifolia* occurs in shallow water when associated with *T. angustifolia*, although it is able to colonise the full range of depths when growing alone (Grace & Wetzel, 1981a).

## GROWTH AND DEVELOPMENT

### Morphology

*Typha* spp. are clonal plants that form stands made of relatively few genetic individuals, known as genets. These are made up of numerous leafy shoots (called ramets) which are linked by an extensive rhizome network. Ramets have a basal meristem which gives rise to both leaves and to inflorescences. Flowering consumes the meristem, halting leaf production. In *T. latifolia* this results in the death of the entire ramet (Grace & Wetzel, 1981b), but rhizome growth continues in most other species (Grace & Wetzel, 1981b). The rhizome apex is flanked by rows of buds, arranged at 180° to one another; each develops either into new shoots or into rhizomes in response to the loss of apical dominance, and is responsible for the maintenance of the viable plant (Finlayson *et al.*, 1983). The growth and development of clones has been studied by Yeo (1964) and Fiala (1971).

There is inter- and intra-specific morphological variation. For example, *T. angustifolia* has longer, thinner leaves and allocates a greater part of its resources to rhizome biomass and sexual reproduction than does *T. latifolia*. The latter tends to be

shorter, has broader leaves and a lower proportion of underground biomass, and produces fewer flowers in similar habitats (Grace, 1989). Both *T. latifolia* and *T. angustifolia* increase maximum height as water depth increases (Grace, 1989). Hybrid morphology tends to be intermediate between parent species, but the hybrid exhibits greater inter-genet morphological variation than its parent species (Smith, 1987). Intraspecific variation is also visible: plants in closed (dense) communities allocate a greater proportion of resources to ramet growth than to flowering, while the reverse is true in open communities (Grace & Wetzel, 1981a).

**Physiology**

Carbon assimilation by *Typha*, a C3 plant, is high, being comparable to that of C4 grasses (McNaughton & Fullem, 1970). McNaughton (1974) has recorded photosynthetic rates of between 300 and 650mg $CO_2$ $cm^{-2}$ $hr^{-1}$ for *T. latifolia*. Photosynthetic rates are highest in young leaves and decrease with leaf age.

Evapotranspiration rates are higher than those of most emergent hydrophytes, but water loss from a uniform stand in the middle of a large water body does not exceed that from an open water area of similar size (Linacre *et al.*, 1970). Water loss is minimised by the waxy leaf cuticle (Marsh, 1955), but increases as the leaves age and stomatal mobility is lost (Roberts, 1987).

Net aboveground production is generally high but varies between climatic zones, being highest in tropical regions (5 to 10kg $m^{-2}$ $yr^{-1}$; Gopal & Masing, 1990). In warm temperate areas, where growth continues throughout the year, annual aboveground production has been estimated at between 1.2 and 2.5kg $m^{-2}$ (Kalk *et al.*, 1979; Roberts, 1987; Howard-Williams, 1980), while in cool temperate areas annual production estimates range between 0.3 and 2.3kg $m^{-2}$ (Neeley &

Davis, 1985; Hill, 1987).

Belowground production is more difficult to measure and there are fewer data available (Gopal & Masing, 1990). These indicate that belowground production is between 0.3 and 3.9kg $m^{-2}$ $yr^{-1}$ (Anderson, 1976; Fiala, 1978; Hill, 1987). Biomass yields from *Typha* grown in paddy-type systems are generally higher than those reported for traditional crops such as maize or rice (Pratt & Andrews, 1980).

Growth of above and belowground structures are directly related to water depth. Weller (1975) found that in *T. latifolia* grown in Iowa, rhizome shooting rate was significantly reduced by water depths >28cm, while shoot growth was inhibited by depths >43cm. Grace & Wetzel (1981c) found that the depth for optimum growth by *T. latifolia* in Michigan was 50cm. Roberts (1987) found that growth of *T. domingensis* was halted when soil moisture fell below field capacity (defined as no free water above the sediment surface - Roberts, 1987). Maximum tolerated water depth appears to be between 1.0 and 1.2m for most species.

*Typha* has a high water demand associated with its large canopy (Roberts, 1987). Nevertheless, stands are able to expand into marginal areas because shoots are physiologically integrated, and there is inter-ramet moisture transport (Roberts, 1987). Resource sharing, which has been reported in other clonal species (e.g. Pitelka & Ashmun, 1985; Salzman & Parker, 1985), enables *Typha* to colonise areas over which there is a resource gradient. The benefit to shoots in marginal areas is, however, to the detriment of donor shoots. Examples of ramet integration include: the efficient system of photosynthate utilisation and redistribution (Hutchings, 1979); adjustment of emergence and mortality rates so that density remains constant despite differences in sowing rate and light intensity (Kays & Harper, 1974), and the integration of rhizome pattern which results in

predictable shoot positioning (Smith & Palmer, 1976).

In common with all emergent species, *Typha* is tolerant of flooding (Thompson, 1985). Leaves can respire under anaerobic conditions for short periods (Laing, 1980) and shoots, even when dead, are able to aerate roots and rhizomes (Sale & Wetzel, 1983; Jordan & Whigham, 1988). The well developed aerenchymatous tissue and continuously open stomata (Cary *et al.*, 1982; Sale & Wetzel, 1983) ensure that oxygen continuously diffuses into roots and rhizomes.

Growth is sensitive to temperature and to nutrient supply (Sharitz *et al.*, 1984). For example, *T. latifolia* has been shown to be most productive at 32°C (Adriano *et al.*, 1980), while production by *T. orientalis* was greatest at 25°C (Cary *et al.*, 1982; Cary & Weerts, 1984). *Typha orientalis* was more productive when nitrogen and phosphorus levels were high (100mgN $l^{-1}$ and 10mgP $l^{-1}$) (Cary *et al.*, 1982; Cary & Weerts, 1984). Tall, dense stands of *Typha* are generally associated with eutrophic systems (Krasnova, 1988; Dykyjova, 1978; Davis, 1991).

*Typha* exhibits ecotypic differentiation in response to temperature (McNaughton, 1974; Mashburn *et al.*, 1978), and to salinity variations (Mashburn *et al.*, 1978; von Oertzen & Finlayson, 1984). Research on the effects of temperature on enzyme levels indicates that *Typha* quantitatively adapts to environmental variation, with single genotypes producing different levels of various enzymes depending on their environment (Jones *et al.*, 1979).

**Phenology and Shoot Development**

The phenological development of *T. latifolia*, *T. angustifolia* and *T. orientalis* has been described by Fiala (1971, 1978), Linde *et al.* (1976), Grace & Wetzel (1981b, 1982a), Dickerman (1982), Lieffers (1983) and Roberts (1987).

Shoots first appear as buds enclosed in sheathing leaves at the rhizome tip. These sprouts contain the meristematic regions which produce leaves and flowers. They are formed during autumn when they are linked to the parent shoot by a short, thick rhizome (Fiala, 1971, 1978). They elongate very slowly and usually only emerge above the ground in the following summer. Soon after emergence the aerial shoots begin to develop. Leaves are formed by the proliferation and elongation of meristematic tissue near the base of the growing leaf. Further growth occurs as the mature tissue is pushed upward by the elongating new tissue. Vegetative shoots are made up entirely of bundles of leaves growing from the subterranean leaf base.

When fruiting heads develop they emerge from the centre of the leaf bundle and are produced on a spadix. The fruiting head first appears in late summer, inhibiting leaf production and elongation. Flowering is a major phenological event which causes marked deviations from the normal growth pattern. For example, flowering shoots are generally shorter than generative shoots, but their growth rate is higher, suggesting that they exercise nutritional and/or hormonal priority within the clonal mass (Waters & Shay, 1991). The staminate spike matures first and releases pollen over a period of approximately one month. When female flowers are fertilised, the pistillate inflorescence increases in diameter as seeds are produced. As these seeds mature the spike changes from being green and velvety, to brown and fluffy.

New rhizomes are also produced during the flowering period. The meristematic region of the rhizome lies directly behind its apex so that cell proliferation and elongation push the tip forward, leaving the mature tissue behind. During the period between flowering and winter senescence, rhizome stores are renewed as nutrients and excess carbohydrates translocate from the aboveground organs.

**Reproduction and Growth**

The *Typha* inflorescence is protandrous and self-fertilisation is likely as pollen falls onto the female flower. The chances of cross-fertilisation increase during windy periods and in species which release pollen as single grains (e.g. *T. latifolia* and *T. capensis*) rather than in tetrads (e.g. *T. angustifolia*) (Krattinger, 1975).

Although only a small percentage of all shoots flower, seed production is extremely high. Krattinger (1975) estimated that each inflorescence produces $0.5 \times 10^6$ seeds, while Yeo (1964) estimated that flowering shoots of *T. latifolia* produced $222 \times 10^3$ seeds $shoot^{-1}$. Wind is the main means of seed dispersal (McNaughton, 1975; Grace & Wetzel, 1981b; Grace, 1987).

On contact with water, the protective seed follicle splits and releases the seed, which sinks (Krattinger, 1975). Seeds can remain viable for long periods (Crocker, 1938, cited in Linde *et al.*, 1976), although viability decreases when relative humidity is low (Sharma & Gopal, 1979; Rivard & Woodard, 1989). Germination increases as light duration and intensity increase. It is inhibited by blue light, but the effect is reversed by red or yellow light (Sharma & Gopal, 1978, 1979; Bonnewell *et al.*, 1983; Galinator & van der Valk, 1986; Rivard & Woodard, 1989; Gopal & Sharma, 1983). Light intensities in excess of 100lux and temperatures as high as 30°C are necessary for germination and seedling establishment in *T. latifolia* (Sharma & Gopal, 1979; Bonnewell *et al.*, 1983). Germination has been reported for both flooded and unflooded seeds (Yeo, 1964; Weller, 1975; Sharma & Gopal, 1979). Despite high germination rates, seedling mortality is high, so that established seedlings are relatively rare in natural habitats (Krattinger, 1983).

Genet growth is by rhizome expansion, which starts

prior to flowering, within the first year of growth. Vegetative expansion is the primary means of reproduction in established *Typha* stands, where germination may be inhibited (Sharma & Gopal, 1978; van der Valk & Davis, 1976; Grace & Wetzel, 1982a). This is typical of clonal species (Cook, 1983).

Vegetative reproduction appears to be greatest during the pioneer phase of stand development, when rhizome connections link more than one parent ramet and their offspring. This indicates more vigorous cloning than in established populations, where rhizome connections are usually only observed between single parent ramets and their daughter shoots (Grace & Wetzel, 1981a).

There is some evidence that rhizome fragments may function as vegetative diaspores (Fiala & Kvet, 1971). Fragments released when sediments are disturbed can be transported to other areas where they may establish new stands. In this way, genets spread along water courses.

**Population Dynamics and Life-History Traits**

Stand development and dynamics have been widely reported for a number of species in cold temperate climates (Mason & Bryant, 1975; Fiala, 1971; White & Sinclair, 1979; Grace & Wetzel, 1981a,b, 1982a,b; Lieffers, 1983; Dickerman & Wetzel, 1985). While there is considerable variation between species, habitat, and latitude, a common pattern can be described for these species. Growth in warmer climates has received less attention (Roberts, 1987).

*Typha* is an effective pioneer species (Weller, 1975; Crook *et al.*, 1984; van der Valk, 1985) and its seeds are generally well represented in wetland seedbanks (Keddy & Reznicek, 1986). Once shoots are established, genets spread rapidly by clonal growth with rhizome expansion proceeding on a wide front (phalanx growth form). The ability to colonise open

spaces has been demonstrated by Yeo (1964), who found that a single ramet produced as many as 98 aerial shoots, colonising an area 3m in diameter, within one growing season, while Marsh (1955) reported that a single genet produced 35 shoots in one season, and that one genet colonised an area of 121ha.

In established stands, new shoots appear among the litter of the previous year's growth. The emergence of sprouts is controlled by temperature and is delayed by late frosts or enhanced in warm, deep water areas or in unshaded, shallow areas. In cool temperate regions, shoots emerge in three main pulses (Dickerman, 1982). The shoots of the first spring pulse mature and die during the year in which they emerge. Most of the mid-summer cohorts also mature and die during their first year. The remainder, together with shoots emerging in late summer, senesce during the winter, but resume development the next spring.

The early formation of a plant canopy gives *Typha* a preemptive advantage in many wetlands. This early spring growth is fuelled by rhizome reserves (Linde *et al.*, 1976; Smith *et al.*, 1988). Any excess reserves, together with current production, is utilised as the largest ramets flower and fruit. The timing of flowering is controlled by photoperiod. Non-flowering shoots continue to grow until lower temperatures initiate shoot senescence and the renewal of rhizome energy reserves during autumn. During winter all aboveground biomass dies and is lost during storms and/or because of frost damage.

The pattern of seasonal development appears to be similar in both tropical and in warm-temperate areas, except that winter die-back is less extensive in the former, and is limited to the death of older shoots. Shoots in their first season may become temporarily senescent, but growth continues throughout the winter period (Roberts, 1987). There have been no studies on

the seasonal changes in rhizome energy stores in warm climates but, because the stands never die back completely, it seems likely that over-wintering stores are less important than in cold climates for reestablishing stand dominance.

The size and number of genets change as stands develop (Krattinger, 1983). Pioneer stands are composed of relatively large numbers of small individuals (i.e. lots of genets with few ramets) but as the number of genets increases, so does competition between them. The less well adapted genets die so that there is a decrease in the number of genets, while the number of ramets per genet of those remaining increases. In senile stands, the number of genets increases again, but competition from other species reduces their size.

Shoot density varies widely and is reported to be highest in eutrophic fishponds and artificial rushbeds (Dykyjova, 1978; Grace, 1989). Under these conditions self-thinning, in the form of high juvenile mortality, has been recorded (Dickerman & Wetzel, 1985). This does not, however, appear to follow the -3/2 Power Law (Dickerman & Wetzel, 1985), as is the case for most clonal species (White, 1985). Instead, they exhibit mortality only after shoot density has approached the theoretical thinning line (Hutchings, 1979; White, 1985).

The colonisation of wetlands by *Typha* species worldwide has been attributed to their "perfect invader status": i.e. they have many of the traits characteristic of invaders (Table 2.1). Morphological and physiological plasticity have been demonstrated by McNaughton (1965, 1966, 1973), Djebrouni & Huon (1988) and Grace & Wetzel (1982a). Further, most species are tolerant of a wide range of environmental conditions (Shay & Shay, 1986; Djebrouni & Huon, 1988; Rivard & Woodard, 1989). Vegetative expansion in *Typha* is also rapid (e.g. Marsh, 1955; Yeo, 1964; Fiala, 1971; Grace & Wetzel, 1981c), and is fuelled by high rates of

**Table 2.1**: The characteristic traits of weeds and invasive plants which are considered the key to their success (Bazzaz, 1984; Baker, 1984; Newsome & Noble, 1986; Arthington & Mitchell, 1986; Ashton & Mitchell, 1989). Those characteristic of *Typha* are marked with *.

| | | |
|---|---|---|
| * | 1. | Morphological, physiological and phenotypic plasticity |
| * | 2. | Environmental tolerance |
| * | 3. | Rapid vegetative growth |
| * | 4. | Fertile and fecund |
| * | 5. | Wide propagule dispersal |
| * | 6. | Competitive life history |
| * | 7. | Life-history versatility |
| * | 8. | Independence of sexual reproduction |
| * | 9. | Large canopy |
| * | 10. | Long-lived rhizomes |
| * | 11 | Energy and nutrient storage capability |
| * | 12. | High regenerative ability |
| * | 13. | Responsive to environmental cues |
| * | 14. | Rapid seedling growth |
| | 15. | Non-specific germination requirements |
| | 16. | Short vegetative phase |
| | 17. | Continuous seed production |
| * | 18. | Self compatible, not obligate self-pollinating or apomictic |
| * | 19. | Wind pollinated or pollinated by a non-specialised flower visitor |
| * | 20. | Tolerant of climatic and edaphic variation |
| * | 21. | Adapted for both long- and short-range dispersal |
| * | 22. | Exhibits some degree of dormancy |
| | 23. | High capacity of acclimation |

photosynthesis (McNaughton, 1974) across the large photosynthetic area (Sale & Orr, 1986; Handoo *et al.*, 1988; Jones, 1988). Although relatively few shoots flower, stand fecundity is also high (Gorbik, 1988) and the single seed fruits are widely dispersed (Watson, 1984; Gorbik, 1988).

*Typha* also exhibits an extremely versatile life-history. It is well adapted as a pioneer species (Crook *et al.*, 1984; Grace & Wetzel, 1981b; Shay & Shay, 1986) and once established is also a powerful competitor (Fiala & Kvet, 1971; Bernard & Gorham, 1978; Pratt *et al.*, 1982). The expansion of established stands is independent of sexual reproduction. This is because the long-lived rhizomes function as perennating organs (McNaughton, 1968; Djebrouni & Huon, 1988), and have remarkable powers of regeneration (Dickerman & Wetzel, 1985).

## ECONOMIC IMPORTANCE

### Detrimental Effects

*Typha* plants, and their dense stands, can cause numerous problems in all types of wetlands. The most often cited are:

- blocking water supply and drainage canals (Finlayson *et al.*, 1983; Grace & Harrison, 1986; van Warmelo, 1989);
- impeding access to water bodies, and interfering with their recreational use (Finlayson *et al.*, 1983; Grace & Harrison, 1986; van Warmelo, 1989);
- altering water flow patterns (Finlayson *et al.*, 1983; Grace & Harrison, 1986; Axelson & Julian, 1988; van Warmelo, 1989);
- invading rice paddies (Finlayson *et al.*, 1983);
- increasing siltation and enhancing "terrestrialisation" (Weisser, 1978; Grace & Harrison, 1986; Gopal & Masing, 1990);
- excessive water loss through evapotranspiration (Grace & Harrison, 1986);

- poisoning of livestock (Grace & Harrison, 1986);
- allergenic reactions in humans to pollen and seeds (Grace & Harrison, 1986; van Warmelo, 1989);
- excluding other wetland species, reducing species and habitat diversity (Beule, 1979; Langley, 1987, 1989; Gopal & Masing, 1990);
- reducing the value of wetlands as waterfowl habitat (Kantrud, 1986; Mallik & Wein, 1986);
- causing fire hazards (Axelson & Julian, 1988);
- acting as a breeding ground for insect vectors, such as the *Anopheles* mosquito (Sculthorpe, 1967; Axelson & Julian, 1988).

**Beneficial Factors**

In the past, *Typha* has been used as a source of food, building material and medicine (Story, 1958; Morton, 1975, 1976; Turner, 1981), and it is still used in the handicraft industry for basketry and for paper-making (Marsh, 1955; Morton, 1975; National Academy of Sciences, 1976). It also has many potential uses including the supply of pulp, fibre, oilseed, human food, stockfeed, thatching, weaving material, and growth regulating substances (Marsh, 1955; Morton, 1975, 1976; Finlayson *et al.*, 1983; Schneider *et al.*, 1983; van der Toorn *et al.*, 1990). There are, however, no documented examples of large commercial concerns utilising their economic potential, although Andrews & Pratt (1978) have investigated the feasibility of growing cattails in a paddy-type agricultural system.

*Typha* is used in aquatic plant systems for treating wastewater (Boyd, 1970; Finlayson & Chick, 1983; Axelson & Julian, 1988), as a bioindicator of heavy metal pollution (Morozov & Torpishcheva, 1977, cited in Finlayson *et al.*, 1983), for reducing soil salinity (Marsh, 1955), as a means of reducing bank erosion (Morton, 1975; Davies, 1981; Axelson & Julian, 1988), and as a supply of bioenergy (Pratt & Andrews, 1980;

Pratt *et al.*, 1982).

In wetlands the most important role of mature, but not senile, stands is to provide habitat for invertebrates and wildlife (Weller, 1975; Cantrell, 1979; Davies, 1981; Gopal & Masing, 1990).

## CONTROL

### Use of Herbicides

*Typha* has been controlled by a number of herbicides including 2,4-D, Monuron, MCPA, TCA, Amitrole, Diuron, 2,2-DPA, Terbutryn and Tandex. Dalapon and Glyphosate are the most widely recommended (Nelson & Dietz, 1960; Robson, 1967; Sculthorpe, 1967; Corns & Gupta, 1971; Agronomy Division, 1973; Weller, 1975; Muir *et al.*, 1981; Finlayson *et al.*, 1983; Grace & Harrison, 1986; Axelson & Julian, 1988; Comes & Kelley, 1989). Most authors recommend that herbicides are applied to foliage, and this is usually done by spraying, although rope-wick application has also been used. Application to the soil is only effective in the absence of standing water (Corns & Gupta, 1971; Grace & Harrison, 1986). Burning the stands prior to treatment improves the efficiency of the herbicide by removing litter (Axelson & Julian, 1988), but even then a second application of herbicide, applied six to eight weeks later, is usually necessary (Sculthorpe, 1967; Axelson & Julian, 1988).

Systemic herbicides are most effective if applied during periods of rapid translocation (Agronomy Division, 1973; Axelson & Julian, 1988); this is when rhizome stores are being accumulated prior to winter die-back, and can be cued as coinciding with pollen release (anthesis) (Linde *et al.*, 1976).

When used in wetlands, most herbicides have environmentally undesirable side-effects, such as reduced plant or animal species diversity (Brooker &

Edwards, 1975; Robson & Barrett, 1977). The long-term side-effects of treatment are unknown (van der Toorn *et al.*, 1990), so mechanical control measures are preferable to using herbicides.

**Cutting, Crushing and Trampling**

A single cut can actually rejuvenate *Typha* stands by removing the litter layer, thereby enhancing shoot emergence (Shekhov, 1974; Gryseels, 1989). Similarly, absolute control has never been reported following the removal of aboveground plant material by repeated cutting (Finlayson *et al.*, 1983). Above-water cuts are most successful when they are timed to coincide with the depletion of rhizome energy reserves (Fiala, 1978; Finlayson *et al*, 1983; Husak *et al.*, 1987), and when they are repeated at frequent intervals to prevent accumulation of reserves (Agronomy Division, 1973; Shekhov, 1974; Grace & Harrison, 1986; Sharma & Kushwaha, 1990). This is because ramet defoliation reduces new rhizome production, which in turn, reduces genet growth (Pitelka & Ashmun, 1985).

Control by physical removal is most successful if the cut shoots are flooded so that the air supply to leaf bases, rhizomes and roots is cut off (Weller, 1975; Beule, 1979; Murkin & Ward, 1980). Anaerobic respiration by these organs produces ethanol, which causes tissue breakdown and rhizome death (Sale & Wetzel, 1983). Nelson & Dietz (1960), Beule (1979) and Jordan & Whigham (1988) have shown that crushing shoots (mechanically or by trampling), so that the bent shoots are flooded, is nearly as effective as cutting as long as all shoot parts are flooded to prevent oxygen diffusion. The effectiveness of flooding is increased when water depths are in excess of 25cm above stubble (Murkin & Ward, 1980).

Traditionally, aquatic weeds have been manually removed from areas where they caused problems (Robson, 1967; Sculthorpe, 1967). This is a slow and expensive

process and today wetland managers can usually afford to treat only small areas by hand. Instead they mechanically clear emergent vegetation after draining the wetland. In areas where sediments cannot be drained adequately, machinery capable of working in wet and muddy conditions is specially commissioned. Mechanical cutting methods are also expensive; van der Toorn *et al.* (1990) estimated that the capital investment in amphibious machinery required to harvest 125 000 tons of reed $yr^{-1}$ for ten years was \$US16 $x10^6$. In 1984, the cost of reed harvesting in Sweden was \$US100 metric ton air dried $reed^{-1}$ (Graneli, 1984, cited in van der Toorn *et al.*, 1990), and Andrews & Pratt (1978) have suggested that harvesting *Typha* will be more costly. For this reason, problem plants should be removed when they begin to invade, rather than after large-scale infestations have occurred.

The physical removal of plants has many advantages. Amongst others, it eliminates all traces of the plants and it reduces the mass of nutrients reentering the sediments, especially if plants are harvested prior to winter translocation (Carpenter & Adams, 1977; Adriano *et al.*, 1980; Cary & Weerts, 1984). It also retards "terrestrialisation" (van der Toorn *et al.*, 1990) and creates open areas within the wetland, thus improving wildfowl habitat (van der Toorn *et al.*, 1990). The primary disadvantage of harvesting methods is that they entail the removal of bird nesting sites and invertebrate substratum. Where inappropriate in terms of wetland management, these effects can, however, be minimised. For example, in wetlands managed for waterfowl, treatment can be limited to the second part of the growing season, when most avian breeding cycles are complete (van der Toorn *et al.*, 1990).

**Fire**

Fire has been used to remove *Typha* stands temporarily, but usually does not control their expansion (Smith, 1989; Ball, 1990). Its effectiveness as a means of

control is greatest if the fire is very hot and is set when the stands are relatively dry. This is because fire damages the apical buds by burning down to the shoot bases (Mallik & Wein, 1986). "Cool" fires, or those set when the shoot bases are flooded, serve only to remove standing litter and to reduce shoot density. This improves their potential as wildlife habitat (Smith, 1989) but, because shading is reduced, it also rejuvenates the stands (Kantrud, 1986; Rivard & Woodard, 1989). However, if the burnt stubble is flooded to drown belowground organs, burning, even with cool fires, can be effective (Nelson & Dietz, 1960; Krusi & Wein, 1988). Burning has other advantages, such as the removal of plant biomass. This reduces sediment accretion and slows succession by retarding "terrestrialisation" (Howard-Williams, 1983; van der Toorn *et al.*, 1990).

**Biological Control**

Claasen (1921) produced a comprehensive list of all insects which parasitise *Typha*. This includes many species of Lepidoptera and Hemiptera which damage the inflorescence while feeding. Other surface feeders and leaf miners are commonly found on *Typha* leaves. Larvae of *Calendra pertinax* are stem borers and also feed on the starchy cortex of the rhizomes. None have been found to cause significant damage to *Typha* stands, and Penko & Pratt (1986) report that insect damage has not been associated with reduced production. However, Martin (1953, cited in Langley, 1987) reported that entire stands were eliminated after being colonised by boring moth larvae (*Arzana* spp.).

Vertebrates that graze on *Typha* include kangaroo, rodents, and water birds in Australia (Finlayson *et al.*, 1983), muskrats in North America (van der Valk & Davis, 1979), and hippopotamus in Africa (Scotcher, 1974). The thick cuticle and fibrous tissues of *Typha* reduce its value as a foodstuff (Smith, 1989), and

grazing is unlikely to reduce production significantly. The physical damage caused by trampling and wallowing may be more effective (Kantrud, 1986; Finlayson *et al.*, 1983) as is muskrat damage during feeding and lodge building (Pelikan *et al.*, 1970; Weller, 1975; Danell, 1979; van der Valk, 1985). In general, vertebrate damage does not control *Typha*, but it may increase habitat heterogeneity by creating clearings which other species of plants (and animals) can exploit (Pelikan *et al.*, 1970).

**Environmental Manipulation**

From an environmental point of view the most acceptable way of controlling *Typha* is to mimic natural processes which inhibit its growth (Ball, 1990) One such mechanism is to stress the plants with rapid and unseasonal fluctuations in water level (Keddy & Reznicek, 1986). This, however, requires detailed knowledge of the environmental requirements of the plant, the hydrology of the infested system as well as the possibility of controlling water levels (Mitchell, 1979, 1985). It has been used most successfully to eliminate submerged weeds, but can be used to inhibit *Typha* growth and bed encroachment, by prolonging floods or extending drought periods (van der Valk & Davis, 1979; Farney & Bookhout, 1982; Keddy & Reznicek, 1986).

Drawdown is a wetland management technique recommended for reducing the dominance of emergent plant stands, while enhancing colonisation by annual species. For complete control of *Typha*, wetlands need to be drained for a minimum of two growing seasons every five to ten years (Nelson & Dietz, 1960; van der Toorn *et al.*, 1990) so that mudflat annuals are able to regenerate. Kuflikowski (1968) has, however, reported that all emergent species disappeared when the wetland water level was reduced for "several months". The success of drawdown as a control method lies in the speed of drying and the length of the dry period, and not in

the change in water level *per se* (Howard-Williams, 1979). Gradual drawdown, especially during the growing season, can actually enhance encroachment (Keddy & Reznicek, 1986; Toivonen & Nybom, 1989). Control is also improved by changes in water and soil chemistry associated with drawdown, notably the increase in salinity (Thompson, 1985), which inhibits germination and seedling establishment (Beare & Jedler, 1987).

The use of drawdown is limited, except in areas with prolonged dry seasons, or in wetlands that can be artificially drained (Sculthorpe, 1967). It also has several short-term disadvantages, including a negative effect on wetland wildlife and concomitant public criticism (van der Toorn *et al.*, 1990).

At the other extreme, flooding has been used to eradicate *Typha* stands (Gopal & Masing, 1990). It is most successful when used in combination with mowing, and is dependent on the proper timing and extent of flooding (Ball, 1990; Chabreck, 1976; Howard-Williams, 1979; Davis & Botch, 1990). Prolonged periods of high water level also kill intact *Typha* shoots: Beule (1979) found that after two years, in areas that were flooded to a depth of 90cm, there was a marked decrease in shoot density, while after three years the stand had died. Flooding to remove *Typha* is most effective in wetlands which do not have gently sloping shorelines which maintain a depth gradient.

An alternative approach to emergent hydrophyte control is to create disturbance by introducing unpredictable, catastrophic hydrological conditions that override seasonal, moderate changes. This approach is used in the marshes of North America, where marked drawdown alternating with high levels of flooding imitates natural hydrological cycles, preventing the development of monospecific plant stands (Weller, 1978; Bishop *et al*, 1979). The optimum amplitudes and frequencies of disturbance necessary to maximise

species diversity are yet to be determined (Keddy & Reznicek, 1986), but are assumed to lie somewhere between that of regular seasonal changes and the massive, unseasonal drawdown observed in reservoirs used for hydroelectric power generation (Keddy & Reznicek, 1986).

**REFERENCES**


ADAMSON, R.S. & SALTER, T.M. 1950. *Flora of the Cape Peninsula*. Juta Press, Cape Town.

ADRIANO, D.C., FULENWIDER, A., SHARITZ, R.R., CIRACALO, T.G. & HOYT, G. 1980. Growth and mineral nutrition of cattail *Typha latifolia* as influenced by thermal alteration. *J. Environ. Qual.*, **9**: 649-453.

AGRONOMY DIVISION, 1973. Cumbungi - a menace to water storage. *Tas. J. Agric.*, **13**: 86-90.

ANDERSON, F.O. 1976. Primary production in a shallow water lake with special reference to a reed swamp. *Oikos*, 27: 243-250.

ANDREWS, N.J. & PRATT, D.C. 1978. Energy potential of cattails (*Typha* spp.) and productivity in managed stands. *J. Minn. Acad. Sci.*, **44**: 5-8.

ARTHINGTON, A.H. & MITCHELL, D.S. 1986. Aquatic invading species. In: *Ecology of Biological Invasions*. Groves, R.H. & Burdon, J.J. (eds). Cambridge University Press, Cambridge.

ASHTON, P.J. & MITCHELL, D.S. 1989. Aquatic plants: Patterns and modes of invasion, attributes of invading species and assessment of control programmes. In: *Biological Invasions: A global perspective*. Drake, J.A., Mooney, H.A., diCastri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. & Williamson, M. (eds). Wiley Press, New York.

AXELSON, S. & JULIAN, C. 1988. Weed control in small dams. Part 1. Introduction: Control of algae and of cumbungi. *Queensland Agric. J.*, **July-Aug**: 241-246.

BAKER, H.G. 1984. Pattern of plant invasion in North America. In: *Ecology of Biological Invasions of North America and Hawaii*. Mooney, H.A. & Drake, J.A. (eds). Springer-Verlag, Berlin.

BALL, J.P. 1990. Influence of subsequent flooding depth on cattail control by burning and mowing. *J. Aquat. Plant Mngmt.*, **28**: 32-36.

BAZZAZ, F.A. 1984. Demographic consequences of plant physiological traits: Some case studies. In: *Perspectives in Plant Population Ecology*. Dirzo, R. & Sarakan, J. (eds). Sinauer Associates Inc., Sunderland.

BEARE, P.A. & JEDLER, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh - the role of salinity intrusion. *Estuaries*, 10: 165-170.

BERNARD, J.M. & GORHAM, E. 1978. Life-history aspects of primary production in sedge wetlands. In: *Freshwater Wetlands: Ecological processes and management potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York, London.

BEULE, J.D. 1979. *Control and Management of cattails in south-eastern Wisconsin wetlands*. Tech. Bull. No. 112, Dept. Nat. Res., Madison, Wisconsin.

BISHOP, R.A., ANDREWS, R.D. & BRIDGES, R.J. 1979. Marsh management and its relation to vegetation, waterfowl and muskrats. *Proc. Iowa Acad. Sci.*, **86**: 50-56.

BONNEWELL, V., KOUKKARI, W.L. & PRATT, D.C. 1983. Light, oxygen and temperature requirements for *Typha latifolia* seed germination. *Can. J. Bot.*, **61**: 1330-1336.

BOUCHER, C. 1988. Wetland vegetation of the Fynbos biome. In: *Hydrology and Hydrobiology in the Fynbos biome*. King, J.M. (ed.). Foundation for Research and Development Occasional Report No. 26, CSIR, Pretoria.

BOYD, C.E. 1970. Vascular aquatic plants for mineral nutrient removal from polluted waters. *Econ. Bot.*, **24**: 95-103.

BROOKER, M.P. & EDWARDS, R.W. 1975. Aquatic herbicides and the control of water weeds. *Water Res.*, **9**: 1-15.

CANTRELL, M.A. 1979. Invertebrate communities in the Lake Chilwa swamp in years of high level. In: *Lake Chilwa: Studies of change in a tropical ecosystem*. Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds). Dr W. Junk Publishers, The Hague.

CARPENTER, S.R. & ADAMS, M. 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: Implications for macrophyte harvesting. *Aquat. Bot.*, **3**: 239-255.

CARY, P.R., FINLAYSON, V.M., MITCHELL, D.S., ORR, P.T., ROBERTS, J. & SALE, P.J.M. 1982. *Biology, management and use of Typha spp. (cumbungi) in Australia*. Research Report 1980-82, CSIRO Division of Irrigation Research, Griffith.

CARY, P.R. & WEERTS, P.G.J. 1984. Growth and nutrient composition of *Typha orientalis* as affected by water temperature and nitrogen and phosphorus supply. *Aquat. Bot.*, **19**: 105-118.

CHABRECK, R.H. 1976. Management of wetlands for wild-life habitat improvement. In: *Estuarine Processes: 1. Uses, stresses and adaption to the estuary*. Wiley, M. (ed.). Academic Press, London.

CLAASEN, P.W. 1921. *Typha* insects: their ecological relationships. *Cornell Univ. Agric. Exp. St. Mem.*, **47**: 463-507.

COMES, R.D. & KELLEY, A.D. 1989. Control of common cattail with post-emergence herbicides. *J. Aquat. Plant Mngmt.*, **27**: 20-23.

COOK, R.E. 1983. Clonal plant populations. *Am. Sci.*, **71**: 244-253.

CORNS, W.S. & GUPTA, R.K. 1971. Chemical control of cattail *Typha latifolia*. *Can. J. Plant Sci.*, **51**: 491-497.

CROOK, C.C., BOAR, R.R. & MOSS, B. 1984. *The decline of reedswamp in the Norfolk Broadland: The importance of rhizome structure*. Broads Authority, BARS 10, East Anglia.

DANELL, K. 1979. Reduction of aquatic vegetation following the colonisation of a northern Swedish lake by the muskrat *Ondatra zibethica*. *Oecol. (Berl.)*, **38**: 101-106.

DAVIES, B.R. 1981. *Management recommendations for the Wilderness Coastal Lakes system*. Unpublished report, Department of Zoology, Rhodes University, Grahamstown.

DAVIS, C.B. & BOTCH, M.S. 1990. Climate. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgensen, S.E. and Dumont, H. (eds). SPB Academic Publishing, The Hague.

DAVIS, S.M. 1991. Growth, decomposition and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat. Bot.*, **40**: 203-224.

DICKERMAN, J.A. 1982. *Pattern and Process of Clonal Growth in a Common Cattail (Typha latifolia* L.). DOE/EV/01599-219-Pt4. NTIS Order No. DE82021971;COO-1599-219-Pt4; Contract AC02-76EV01599.

DICKERMAN, J.A. & WETZEL, R.G. 1985. Clonal growth in *Typha latifolia*: Population dynamics and demography of the ramets. *J. Ecol.*, **73**: 535-552.

DJEBROUNI, M. & HUON, A. 1988. Structure and biomass of a *Typha* stand revealed by multidimensional analysis. *Aquat. Bot.*, **39**: 331-342.

DYKYJOVA, D. 1978. Nutrient uptake by littoral communities of helophytes. In: *Pond Littoral Ecosystems: Structure and functioning*. Dykyjova, D. & Kvet, J. (ed.). Ecological Studies, **28**. Springer-Verlag, Berlin.

FARNEY, R.A. & BOOKHOUT, T.A. 1982. Vegetation changes in a Lake Erie marsh (Winous Point, Ottawa Country, Ohio) during high water years. *Ohio J. Sci.*, **82**: 103-107.

FIALA, K. 1971. Seasonal changes in the growth of clones of *Typha latifolia* L. in natural conditions. *Folia Geobot. Phytotaxon.*, **6**: 225-270.

FIALA, K. 1978. Underground organs of *Typha angustifolia* and *Typha latifolia*: Their growth, propagation and production. *Prirodoven. Pr. Ustavu. Cesk. Akad. Ved. Brne.*, **12**: 1-43.

FIALA, K. & KVET, J. 1971. Dynamic balance between plant species in South Moravian reedswamps. In: *The Scientific Management of Animal and Plant Communities for Conservation*. Duffey, E. & Watt, A.S. (eds). Blackwell Scientific Publications, Oxford.

FINLAYSON, C.M. & CHICK, A.J. 1983. Testing the potential of aquatic plants to treat abattoir effluent. *Water Res.*, **17**: 414-422.

FINLAYSON, C.M., ROBERTS, J., CHICK. A.J. & SALE, P.J.M. 1983. Biology of Australian weeds. II. *Typha domingensis* Pers. and *Typha orientalis* Presl. *J. Aust. Inst. Aust. Weeds*, **49**: 3-10.

GALINATOR, M.I. & VAN DER VALK, A.G. 1986. Seed germination traits of annual and emergents recruited during drawdown in the Delta Marsh, Manitoba, Canada. *Aquat. Bot.*, **26**: 89-102.

GOPAL, B. & SHARMA, K.P. 1983. Light regulated seed germination in *Typha angustata* Bory et Chaub. *Aquat. Bot.*, **16**: 377-384.

GOPAL, B. & MASING, V. 1990. Biology and ecology. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgensen, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

GORBIK, V.P. 1988. Seed production of *Typha angustifolia* in Dnieper Reservoirs. *Hydrobiol. J.*, **24**: 55-59.

GRACE, J.B. 1985. Juvenile vs. adult competitive abilities in plants: Size-dependence in cattails (*Typha*). *Ecology*, **66**: 1630-1638.

GRACE, J.B. 1987. The impact of pre-emption on the zonation of two *Typha* species along lake shores. *Ecol. Monogr.*, **57**: 283-303.

GRACE, J.B. 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *Am. J. Bot.*, **76**: 762-768.

GRACE, J.B. & HARRISON, J.S. 1986. The biology of Canadian weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha glauca* Godr. *Can. J. Plant Sci.*, **66**: 361-379.

GRACE, J.B. & WETZEL, R.G. 1981a. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies of the intensity of competition. *Am. Nat.*, **118**: 463-474.

GRACE, J.B. & WETZEL, R.G. 1981b. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia*: Experimental studies in marshes of differing successional maturity. *Ecology*, **62**: 789-801.

GRACE, J.B. & WETZEL, R.G. 1981c. Effect of size and growth rate on vegetative reproduction in *Typha*. *Oecol. (Berl.)*, **50**: 158-161.

GRACE, J.B. & WETZEL, R.G. 1982a. Variations in growth and reproduction within populations of two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Oecol. (Berl.)*, **53**: 258-263.

GRACE, J.B. & WETZEL, R.G. 1982b. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Can. J. Bot.*, **60**: 46-57.

GRYSEELS, M. 1989. Nature management experiments in a derelict reedmarsh. 1. Effect of winter cutting. *Biol. Cons.*, **47**: 171-193.

HANDOO, J.K. SARAF, N. & KAUL. V. 1988. Energy content and ecological efficiency of macrophytes in Dal Lake, Kashmir. *Arch. Hydrobiol.*, **111**: 351-367.

HILL, B.H. 1987. *Typha* production in a Texas pond: Implications for energy and nutrient dynamics in freshwater wetlands. *Aquat. Bot.*, **27**: 385-394.

HOWARD-WILLIAMS, C. 1979. The distribution of aquatic macrophytes in Lake Chilwa: Annual and long-term fluctuations. In: *Lake Chilwa: Studies of change in a tropical ecosystem*. Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds). Dr W. Junk Publishers, The Hague.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophyte communities of the Wilderness Lakes: Community structure and associated environmental conditions. *J. Limnol. Soc. sth. Afr.*, **6**: 85-92.

HOWARD-WILLIAMS, C. 1983. Wetlands and watershed management; the role of aquatic vegetation. *J. Limnol. Soc. sth. Afr.*, **9**: 54-62.

HUSAK, S., KVET, J. & PLASENCIA FRAGA, J.M. 1987. Experiments with mechanical control of *Typha* spp. stands. *Proceedings of the 7th International Symposium on Aquatic Weeds*. Loughborough. E.W.R.S., Wageningen.

HUTCHINGS, M. 1979. Weight-density relationships in a ramet population of clonal perennial herbs, with special reference to the -3/2 power law. *J. Ecol.*, **67**: 21-23.

JONES, J.C., HANCOCK, J.F. & LIU, E.H. 1979. Biochemical and morphological effects of temperature on *Typha latifolia* (Typhaceae) originating from different ends of a thermal gradient. 1. Controlled environmental studies. *Am. J. Bot.*, 66: 902-906.

JONES, M.B. 1988. Photosynthestic responses of C3 and C4 wetland species in a tropical swamp. *J. Ecol.*, 76: 253-262.

JORDAN, T.E. & WHIGHAM, D.F. 1988. The importance of standing dead shoots of the narrow-leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, 29: 319-328.

KALK, M.J., MCLACHLAN, A.J. & HOWARD-WILLIAMS, C. (eds). 1979. *Lake Chilwa: Studies of change in a tropical ecosystem.* Monogr. Biol., 35: Dr W. Junk Publishers, The Hague.

KANTRUD, H.A. 1986. *Effects of vegetation manipulation on breeding waterfowl in Prairie wetlands - a literature review.* Fish and Wildlife Technical Report 3, Washington D.C.

KAYS, S. & HARPER, J.L. 1974. The regulation of plant and tiller density in a grass sward. *J. Ecol.*, 62: 97-105.

KEDDY, P.A. & REZNICEK, A.A. 1986. Great Lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. *J. Great Lakes Res.*, 12: 25-36.

KRASNOVA, A.N. 1988. *Ecology* and phytocenology of species of the genus *Typha* in lakes of the North Dvina Basin. *Hydrobiol. J.*, 24: 7-10.

KRATTINGER, K. 1975. Genetic mobility in *Typha*. *Aquat. Bot.*, 1: 57-70.

KRATTINGER, K. 1983. Estimation of size and number of individual plants within populations of *Typha latifolia* L. using isoelectrofocusing. *Aquat. Bot.*, 15: 241-247.

KRATTINGER, K., RAST, D. & KARESCH, H. 1979. Analysis of pollen proteins of *Typha* species in relation to identification of hybrids. *Biochem. Syst. Ecol.*, 7: 125-128.

KRUSI, B.O. & WEIN, R.W. 1988. Experimental studies of the resiliency of floating *Typha* mats in a freshwater marsh. *J. Ecol.*, 76: 60-72.

KUFLIKOWSKI, T. 1968. Vegetation of the Goczalkowice Dam reservoir in the years 1964-1966. *Acta Hydrobiol.*, 10: 165-178.

LAING, H.E. 1980. Respiration of the leaves of *Nuphar advenum* and *Typha latifolia*. *Am. J. Bot.*, 27: 583-586.

LANGLEY, C.H. 1987. *Notes on Typha latifolia: A threat to our wetlands.* Unpublished report. Rondevlei Bird Sanctuary, Cape Town.

LANGLEY, C.H. 1989. Problems caused by *Typha*. In: *Typha: Its status, problems, economic benefits and control.* van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

LIEFFERS, V.J. 1983. Growth of *Typha latifolia* in Boreal forest habitats, as measured by double sampling. *Aquat. Bot.*, 15: 335-348.

LINDE, A.F., JANISCH, T. & SMITH, D. 1976. *Cattail: The significance of its growth, phenology and carbohydrate storage to its control and management.* Tech. Bull. 94. Department of Natural Resources, Madison, Wisconsin.

MALLIK, A.U. & WEIN, R.W. 1986. Response of a *Typha* marsh to draining, flooding and seasonal burning. *Can. J. Bot.*, **64**: 2136-2143.

MARSH, L.C. 1955. The cattail story. *Garden J.*, **5**: 114-129.

MASHBURN, S.J., SHARITZ, R.R. & SMITH, M.H. 1978. Genetic variation among *Typha* populations of the south-eastern United States. *Evolution*, **32**: 681-685.

MASON, C.F. & BRYANT, R.J. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, **63**: 71-95.

MCNAUGHTON, S.J. 1965. Differential enzymatic activity in ecological races of *Typha latifolia* L. *Science*, **150**: 1829-1830.

MCNAUGHTON, S.J. 1966. Ecotypic function in the *Typha* community type. *Ecol. Monogr.*, **36**: 297-325.

MCNAUGHTON, S.J. 1968. Autotoxic feedback in the regulation of *Typha* populations. *Ecology*, **49**: 367-369.

MCNAUGHTON, S.J. 1973. Comparative photosynthesis of Quebec and California ecotypes of *Typha latifolia*. *Ecology*, **54**: 1260-1270.

MCNAUGHTON, S.J. 1974. Developmental control of net productivity in *Typha latifolia* ecotypes. *Ecology*, **55**: 864-869.

MCNAUGHTON, S.J. 1975. r- and k- selection in *Typha*. *Am. Nat.*, **109**: 251-261.

MCNAUGHTON, S.J. & FULLEM, L.W. 1970. Photosynthesis and photorespiration in *Typha latifolia*. *Plant Physiol.*, **45**: 703-707.

MITCHELL, D.S. 1979. Formulating aquatic weed management programmes. *J. Aquat. Plant Mngmt.*, **17**: 22-24.

MITCHELL, D.S. 1985. African aquatic weeds and their management. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, The Hague.

MORTON, J.F. 1975. Cattails (*Typha* spp.) - Weed problem or potential crop. *Econ. Bot.*, **29**: 7-29.

MORTON, J.F. 1976. Craft industries from coastal wetland vegetation. In: *Estuarine Processes. 1. Uses, stresses and adaptions to the estuary*. Wiley, M. (ed.). Academic Press, New York.

MUIR, D.C.G., PITZE, M., BLOUW, A.P. & LOCKHART, W.L. 1981. Fate of terbutryn in macrophyte-free and macrophyte-containing farm ponds. *Weed Res.*, **21**: 59-70.

MURKIN, H.R. & WARD, P. 1980. Early spring cutting to control cattail in a northern marsh. *Wildl. Soc. Bull.*, **8**: 254-256.

NAPPER, D.M. 1971. Typhaceae. *Flora Trop. East Afr.*

NATIONAL ACADEMY OF SCIENCE, 1976. *Making Aquatic Weeds Useful. Some Perspectives for Developing Countries*. Washington D.C.

NEELEY, R.K. & DAVIS, C.B. 1985. Nitrogen and phosphorus fertilisation of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. 1. Emergent plant production. *Aquat. Bot.*, **22**: 347-361.

NELSON, N.F. & DIETZ, R.H. 1960. *Cattail Control Methods in Utah*. Utah State Department of Fish and Game Publication No. 66-2.

NEWSOME, A.E. & NOBLE, I.R. 1986. Ecological and physiological characters of invading species. In: *Ecology of Biological Invasions*. Groves, R.H. & Burdon, J.J. (eds). Cambridge University Press, Cambridge.

PELIKAN, J., SVOBODA, J. & KVET, J. 1970. On some relations between the production of *Typha latifolia* and a muskrat population. *Zool. Listy*, 19: 303-329.

PENKO, J.M. and PRATT, D.C. 1986. Effects of *Bellura obliqua* on *Typha latifolia* productivity. *J. Aquat. Plant Mngmt.*, 24: 24-28.

PITELKA, A. & ASHMUN, J.W. 1985. Physiology and integration of ramets in clonal plants. In: *Population Biology and Evolution of Clonal Organisms*. Jackson, J.B.C., Buss, L.W. & Cook, R.E. (eds). Yale University Press, New Haven.

PRATT, D.C. & ANDREWS, N.J. 1980. Cattails (*Typha* spp.) as an energy source. In: *Energy from Biomass and Wastes*. White, J.W., McGrew, W. & Suttor, M.R. (eds). Florida.

PRATT, D.C., ANDREWS, N.J., DUBBE, D.R., GARVER, E.G., PENKO, M., READ, P.E. & ZIMMERMAN, E.S. 1982. *Emergent aquatics: Stand establishment, management and species screening*. Final Report for the Solar Research Institute, Subcontract No. XK-1087-1.

RIVARD, P.G. & WOODARD, P.M. 1989. Light, ash and pH effects on the germination and seedling growth of *Typha latifolia* (cattail). *Can. J. Bot.*, 67: 2783-2787.

ROBERTS, J. 1987. *The autocology of Typha spp. in south-eastern Australia*. PhD Thesis, University of Adelaide, Australia.

ROBSON, T.O. 1967. Accurate aerial applications of Dalapon to drainage ditches in Britain. *Down to Earth*, Fall: 12-14.

ROBSON, T.O. & BARRETT, P.R.F. 1977. Review of the effects of aquatic herbicides. In: *Ecological Effects of Herbicides*. Perring, F.H. & Mellenby, K. (eds). Academic Press, London.

SALE, P.J. & ORR, P.T. 1986. Gas exchange of *Typha orientalis* Presl. communities in artificial ponds. *Aquat. Bot.*, 23: 309-320.

SALE, P.J. & WETZEL, R.G. 1983. Growth and metabolism of *Typha* species in relation to cutting treatments. *Aquat. Bot.*, 15: 321-334.

SALZMAN, A.G. & PARKER, M.A. 1985. Neighbours ameliorate local salinity stress for rhizomatous plant in a heterogenous environment. *Oecol. (Berl.)*, 65: 273-277.

SCHNEIDER, J.A., YOSHIHARA, K. & NAKANISHI, K. 1983. Typhasterol (2-deoxycasterone): A new plant growth regulator from cattail protein. *Tetragedron Letters*: 24: 3859-3860.

SCOTCHER, J.S.B. 1974. *A quantitative assessment of the food preferences of Hippopotamus amphibious L. in the Ndumu Game Reserve, Tongaland*. MSc Thesis, University of Natal, Pietermaritzburg, South Africa.

SCULTHORPE, C.D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold Publishers, London.

SHARITZ, R.R., ADRIANO, D.C., PINDER, J.E., LUVALL, J.C. & CIRAVOLO, T.G. 1984. Growth and mineral nutrition of cattails inhabiting a thermally -graded South Carolina reservoir. 1. Growth and the macronutrients. *J. Plant Nut.*, **7**: 1671-1698.

SHARMA, K.P. 1978. Effect of cutting on the growth and flowering behaviour of *Typha elephantina* Roxb. *Current Sci.*, **47**: 275-276.

SHARMA, K.P. & GOPAL, B. 1978. Seed germination and occurrence of seedlings of *Typha* species in nature. *Aquat. Bot.*, **4**: 353-358.

SHARMA, K.P. & GOPAL, B. 1979. Effect of water regime on the growth and establishment of *Typha angustifolia* seedlings. *Int. J. Ecol. Environ. Sci.*, **5**: 69-74.

SHARMA, K.P. & GOPAL, B. 1980. A note on the identity of *Typha elephantina* Roxb. *Aquat. Bot.*, **9**: 381-387.

SHARMA, K.P. & KUSHWAHA, S.P.S. 1990. Effects of cutting aboveground organs of *Typha angustata* Bory and Chaub on its growth and total chlorophyll content. *Aquat. Bot.*, **36**: 293-296.

SHAY, J.M. & SHAY, C.T. 1986. Prairie marshes in western Canada, with special reference to the ecology of five emergent macrophytes. *Can. J. Bot.*, **64**: 443-454.

SHEKHOV, A.G. 1974. Effect of cutting time on the renewal of stands of reed and cattail. *Hydrobiol. J.*, **10**: 45-48.

SMITH, A.P. & PALMER, J.O. 1976. Vegetative reproduction and close packing in a successional plant species. *Nature (Lond.)*, **261**: 232-233.

SMITH, C.S., ADAMS, M.S. & GUSTAFSON, T.D. 1988. The importance of belowground mineral element stores in cattails (*Typha latifolia* L.). *Aquat. Bot.*, **30**: 343-352.

SMITH, L.M. 1989. Effects of grazing and burning on the nutritive quality of cattail in Playas. *J. Aquat. Plant Mngmt.*, **27**: 51-53.

SMITH, S.G. 1967. Experimental and natural hybrids in North American *Typha* (Typhaceae). *Am. Midl. Nat.*, **78**: 257-287.

SMITH, S.G. 1987. *Typha*: Its taxonomy and the ecological significance of its hybrids. *Erg. Limnol.*, **27**: 129-138.

STORY, R. 1958. Some plants used by the bushmen in obtaining food and water. *Bot. Surv. Mem.*, **30**. Dept. Agric., Pretoria.

THOMPSON, K. 1985. Emergent plants of permanent and seasonally flooded wetlands. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, The Hague.

TOIVONEN, H. & NYBOM, C. 1989. Aquatic vegetation and its recent succession in the waterfowl wetland Koijarvi, S. Finland. *Ann. Bot. Fennici.*, **26**: 1-14.

TURNER, N.J. 1981. A gift for the taking: The untapped potential of some food plants of North American native peoples. *Can. J. Bot.*, **59**: 2331-2357.

VAN DER TOORN, J., VERHOEVEN, J.T.A. & SIMPSON, R.L. 1990. Freshwater marshes. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgenson, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

VAN DER VALK, A.G. 1985. Vegetation dynamics of prairie glacial marshes. In: *The Population Structure of Vegetation*. White, J. (ed.). Dr W. Junk Publishers, The Hague.

VAN DER VALK, A.G. & DAVIS, C.B. 1976. The seed banks of prairie glacial marshes. *Can. J. Bot.*, **54**: 1832-1838.

VAN DER VALK, A.G. & DAVIS, C.B. 1979. A reconstruction of the recent vegetational history of a Prairie marsh, Eagle Lake, Iowa, from its seed bank. *Aquat. Bot.*, **6**: 29-51.

VAN WARMELO, W. (ed.). 1989. *Typha: Its status, problems, economic benefits and control*. Report on the *Typha* Symposium. Botanical Society of South Africa, Cape Town.

VON OERTZEN, I. & FINLAYSON, C.M. 1984. Wastewater treatment with aquatic plants: Ecotypic differentiation of *Typha domingensis* seedlings. *Environ. Poll.*, **35**: 259-269.

WATERS, I. & SHAY, J.M. 1991. A field study of the effects of water depth, order of emergence and flowering on the growth of *Typha glauca* shoots using the Richard's model. *Aquat. Bot.*, 39: 231-242.

WATSON, L. 1984. *Heaven's Breath. A natural history of the wind*. Hodder and Staughton Ltd., London.

WEISSER, P.J. 1978. A conceptual model of a siltation system in shallow lakes with littoral vegetation. *J. Limnol. Soc. sth. Afr.*, 4: 145-149.

WELLER, M.W. 1975. Studies of cattail in relation to management for marsh wildlife. *Iowa State J. Res.*, **49**: 383-412.

WELLER, M.W. 1978. Management of freshwater marshes for wildlife. In: *Freshwater Wetlands*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

WHITE, J.M. 1985. The thinning rule and its application to mixtures of plant populations. In: *Studies on Plant Demography*. White, J. (ed.). Academic Press, London.

WHITE, J.M. & SINCLAIR, L.R. 1979. Effect of plant spacing on growth and yield of transplanted cattails. *Proc. Soil Crop Sci. Florida*, 38: 18-20.

YEO, R.R. 1964. Life-history of the common cattail. *Weeds*, 12: 284-328.

# CHAPTER 3

# THE DISTRIBUTION AND ENCROACHMENT OF *TYPHA CAPENSIS* IN SOUTH-WESTERN CAPE WETLANDS


## SUMMARY

The primary objective of this chapter is to report on work undertaken to establish whether or not *Typha capensis* is spreading between, and encroaching into, the wetlands of the Cape Flats. The distribution of rushbeds was determined during a survey which included all large permanent, and most small temporary, wetlands. The status of rushbeds (encroaching or stable) was evaluated using aerial photographs, management records (from the Cape Town City Council, Milnerton Municipality and Divisional Council of the Cape) and anecdotal accounts. Together with physical and chemical data, these were used to isolate factors which may promote or hinder local encroachment. Results showed that *Typha* is widespread, but restricted to areas where sediments remain damp during summer. It was not found in wetlands which have steep banks (>60° slope), high salinity (>1°/oo) and/or prolonged periods of deep water (>1.5m). Encroachment by rushes was observed in many wetlands and appeared to be enhanced by reduced seasonal fluctuations in water-level fluctuations. In Rondevlei, where the spread of a single bed was mapped over a two-year period, the growing front of a rushbed encroached at a mean rate of 1.5m $month^{-1}$. The status of the species as a "weed" is discussed. It is concluded that it is not the species, but the life-form (monospecific emergent plant stands), that causes a management problem. These stands are largely the result of anthropogenic alteration of the wetland environment. Thus artificial stabilisation of water level should be eliminated if encroachment is a management problem. The long-term solution to the problem of encroachment in local vleis lies in adoption of a management strategy that reintroduces hydrological disturbance, thus promoting competitive replacement and delaying hydrosere succession.


## INTRODUCTION

The extent to which vegetation develops in a fresh-water body is determined primarily by basin

morphometry (Shay & Shay, 1986). Shallow, gently sloping basins support larger and more diverse populations than those with deep steep-sided banks (Godshalk & Barko, 1985). The species composition of the plant community depends on the physical characteristics of the substratum, basin hydrology, water transparency, soil chemistry and nutrient levels (Roman *et al.*, 1985; Johnson *et al.*, 1985; Kenkel, 1987). Within a typical littoral zone a range of species is usually found. Emergent macrophytes generally dominate the damp unflooded zone and are replaced by submerged hydrophytes in the permanently flooded photic zone (Denny, 1985). Changes in bank structure (sediment type, slope, light climate) create variations which favour different species, resulting in the formation of a mosaic of communities (Whigham & Simpson, 1976, cited in Roberts, 1987).

Emergent species usually appear where environmental conditions meet their germination and establishment requirements. For example, bulrushes germinate on damp sandbanks, where they can become established if they are not inundated early in their development (Grace, 1984). Optimum growth occurs when the plants have a stable water supply, high nutrient level, and are unshaded. Under these conditions, the high rate of vegetative spread ensures quick colonisation of suitable adjacent areas by the rushes. Their competitive growth form inhibits the growth of other macrophytes, and monospecific rushbeds develop.

Optimal growth conditions for *Typha* are typical of many southern Cape Flats wetlands, so it is not surprising that rushbeds have been successful in this area. *Typha capensis*, considered indigenous to the Cape (Napper, 1971), has been widespread for many years (Stephens, 1929). It is, however, only recently that rushbeds have been perceived as a problem, usually because they appear to have spread into, or around a specific wetland (Langley, 1989; Thornton & Boddington, 1989). Despite this perception there is

no evidence to support these claims. Without details regarding where, when, why, and at what rate the beds are spreading, wetland managers have found it difficult to develop management programmes preventing *T. capensis* (hereafter referred to as *Typha*) "encroachment".

The objective of this chapter is to provide data on the distribution and potential rate of spread of *Typha* stands. This information is necessary for the formulation of a successful management programme and to establish whether or not *Typha* is a problem on the Cape Flats. The following questions are addressed in this chapter:

1. What is the present distribution of *Typha* on the Cape Flats?
2. Are the rushbeds spreading, and if so, at what rate?
3. What factors appear to be promoting rushbed encroachment within local wetlands?
4. Is *Typha* the real problem in local wetlands, or is encroachment a reflection of poor wetland management practices?

## THE STUDY AREA

The study area is delimited by the Atlantic coastline to the west, the Kuils River to the east, the Blaauwberg Road to the north and the road between Simonstown and Kommetjie to the south (Fig. 3.1). This area includes a large proportion of the Cape Flats (the lowlands lying between the Cape Peninsula Mountain Range to the west and the Hottentots-Holland Range to the east - Brummer, 1981) where *Typha* is considered to be encroaching, as well as areas to the west of the Flats where rushbeds are found, but where they are not perceived to be problematic. The area has been described in detail by Taylor (1978).

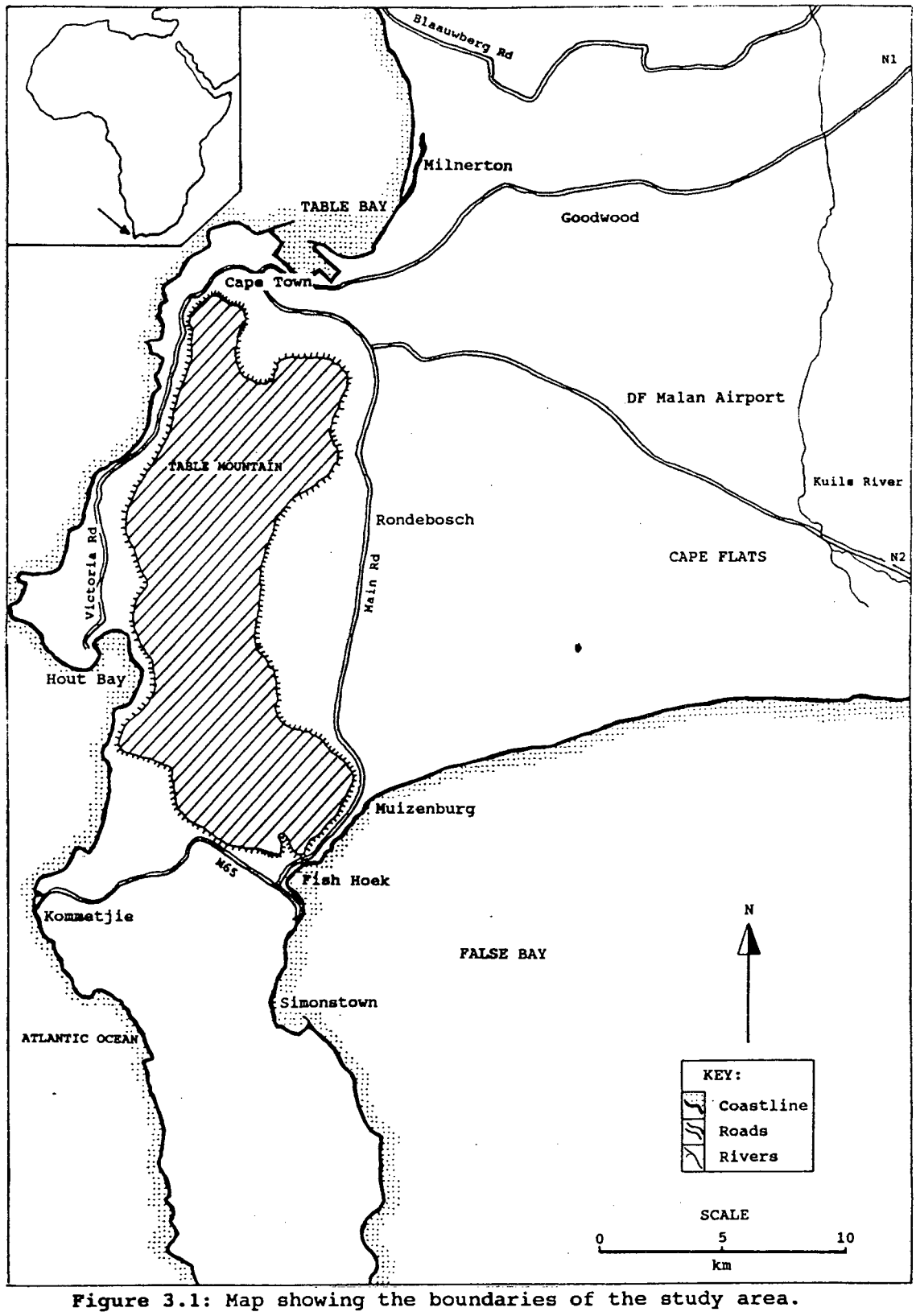



**Figure 3.1:** Map showing the boundaries of the study area.

## GEOLOGY AND SOILS

The geology (Fig. 3.2a) and soils (Fig. 3.2b) of the area are relatively simple. The coastal lowlands consist of fine- to coarse-grained sands of Cenozoic origin, while the coastal dunes generally comprise calcareous alkaline soils with a distinct horizon of lime accumulation. Inland of the dunes there are well-leached acidic soils which are quartzitic in nature, and which include some peat lenses. The area to the west of the Flats comprises Table Mountain Sandstone (TMS), which is well weathered and which forms acidic soils of low fertility. The soils of the northern part of the study area are generally deep acidic sands derived from the Malmesbury group (Day *et al.*, 1979).

## CLIMATE

The study area lies in the Cape region which has a temperate Mediterranean climate (Taylor, 1978), characterised by cold wet winters and warm dry summers. Mean minimum and maximum air temperatures are respectively 8.3°C (July) and 26°C (January). Rainfall during winter is associated with northerly winds caused by low pressure polar air masses which bring in cyclonic storms. Annual totals of between 550 and 750mm have been recorded over the Cape Peninsula (Brummer, 1981). Summers are dry and windy, with strong southerly winds predominating (Brummer, 1981).

## VEGETATION

The south-western Cape comprises one of five Mediterranean regions which have a distinctive flora dominated by evergreen, sclerophyllous shrubs and trees and which develop on nutrient poor soils (Taylor, 1978). The vegetation formation characteristic of the area, known as the Fynbos Biome, is particularly rich in species with an average of

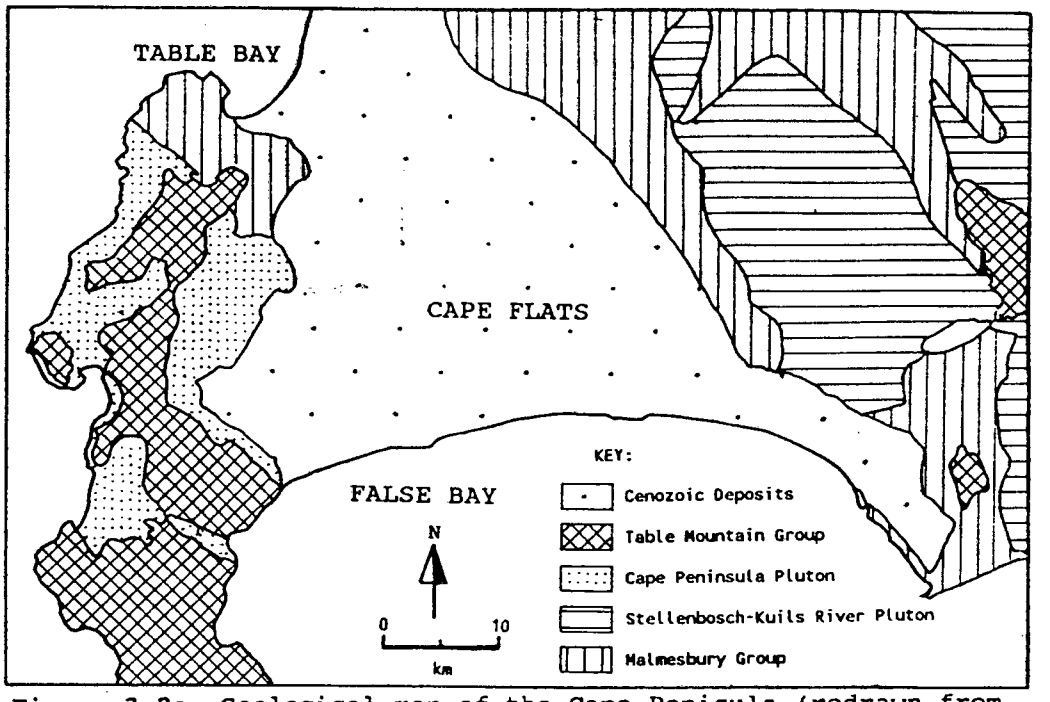



**Figure 3.2a:** Geological map of the Cape Penisula (redrawn from Brummer, 1981).

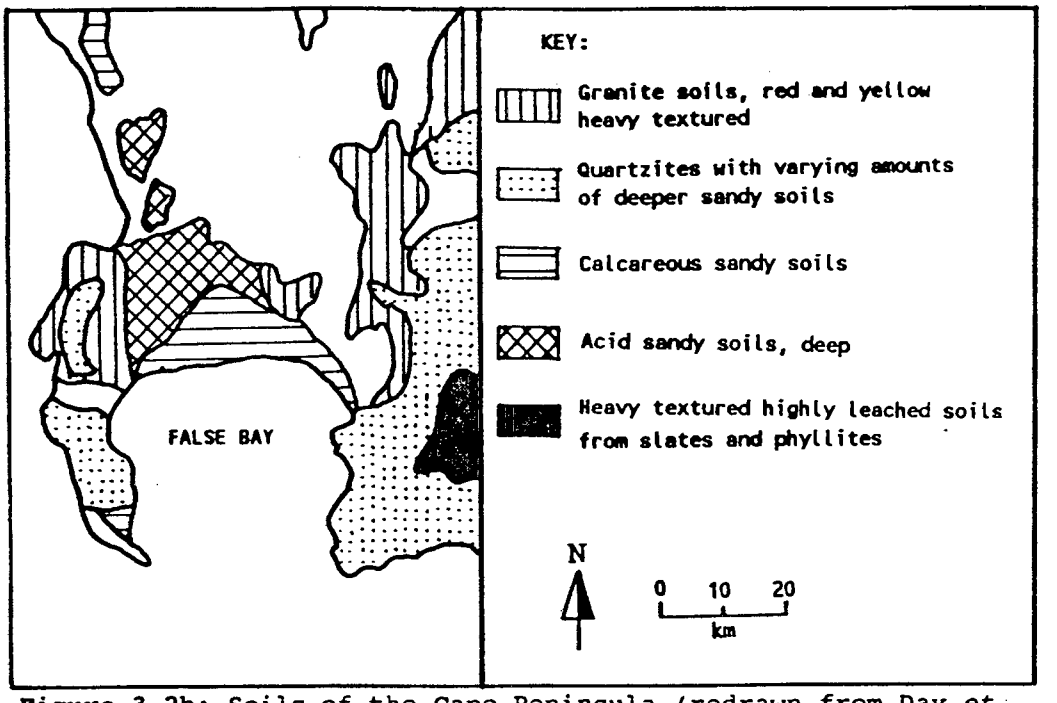



**Figure 3.2b:** Soils of the Cape Peninsula (redrawn from Day *et al.*, 1979).

5 species $km^{-2}$, and more than 200 endemic species recorded within the relatively small area over which Fynbos is found (Grindley, 1984, 1988).

Three of the four recognised types of Fynbos are found in the study area (Fig. 3.3). Strandveld, dominated by broad-leaved shrubs, is confined to the dune regions, while Coastal Fynbos, dominated by Proteaceae, Restionaceae and ericoid-leaved shrubs, is found further inland on the Flats. Mountain Fynbos dominates the areas on TMS. A large portion of indigenous vegetation in the study area has been lost as a result of development. In 1652 most of the Cape Flats was covered with Coastal Fynbos, with Strandveld colonising the dunes. Mountain Fynbos covered the area west of the Flats (Parker, 1982). By 1982 most of the Coastal Fynbos had disappeared, while Strandveld was reduced to a narrow coastal strip along the southern coastal region, and Mountain Fynbos was found only in isolated patches in the northern Peninsula (Fig. 3.3). In most areas indigenous vegetation has been cleared for urban development. Other areas are subject to invasion by alien *Acacia* spp.

Wetlands of the region have typical plant communities (Boucher, 1988), the composition of which is usually determined by salinity. In general, the vegetation of temporary pools is richer and more varied than that of permanent standing waters (Stephens, 1929). Details of wetland vegetation types are discussed later, under the descriptions of major wetlands of the area.

**AQUATIC SYSTEMS**

The study area included a number of water bodies with their associated wetlands (Fig. 3.4). They can be divided into four categories (Stephens, 1929):

1. seasonal wetlands and pools (pans);
2. permanent wetlands and shallow lakes (vleis)
3. streams and rivers, and

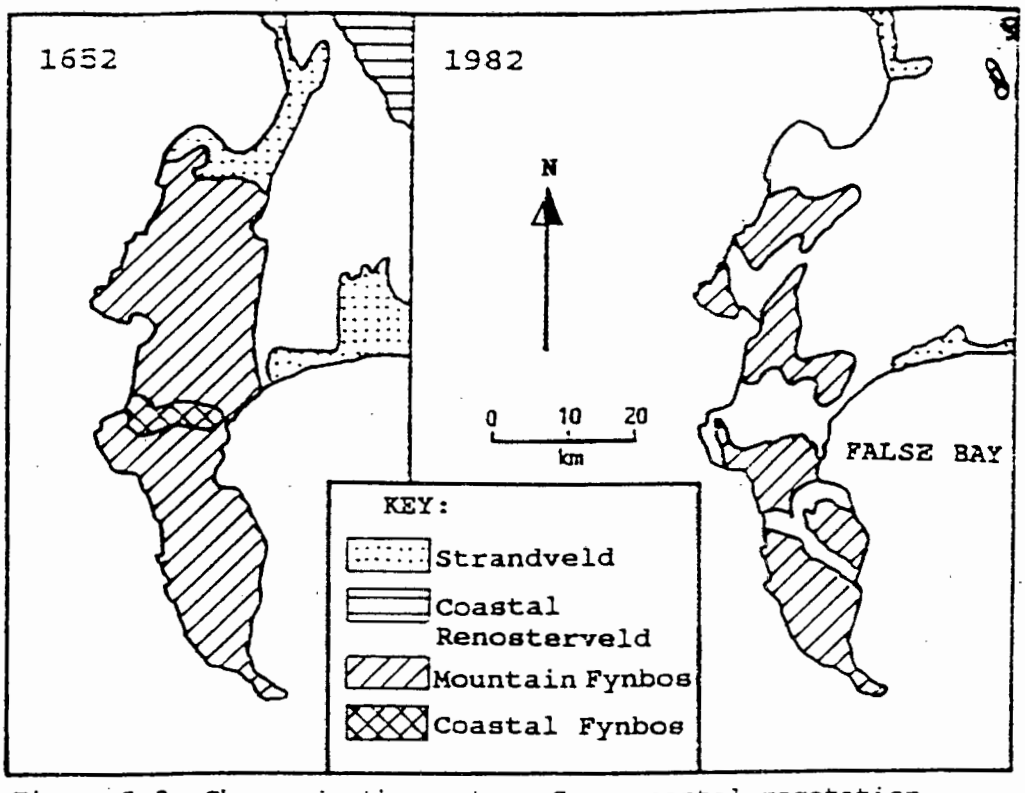



Figure 3.3: Change in the western Cape coastal vegetation between 1652 and 1982 (redrawn from Parker, 1982).

4. reservoirs.

The terms "vlei" and "pan" are local ones. In the Cape, "vlei" refers to any permanent expanse of water, whether open or marshy, while "pan" describes small seasonal pools or damp depressions. The principal vlei and river systems of the study area are indicated in figure 3.4. Most of these have been studied, but little is known about the smaller temporary wetlands.

**Wetlands**

There are five large vlei systems in the study area: the Rietvlei-Milnerton lagoon system, the Rondevlei-Zeekoevlei-Princessvlei system; the Little Princessvlei-Langvlei-Zandvlei system; the Fish Hoek Bay wetlands; and the Papkuilsvlei-Wildevoelvlei-Noordehoek Salt Pans system (Fig. 3.4). They are generally regarded as being polluted, usually because of nutrient enrichment, and siltation is common (Howard-Williams, 1976; Day & King, 1980). In general, the vleis on the Cape Flats are considered to be more disturbed than those on the western side of the study area.

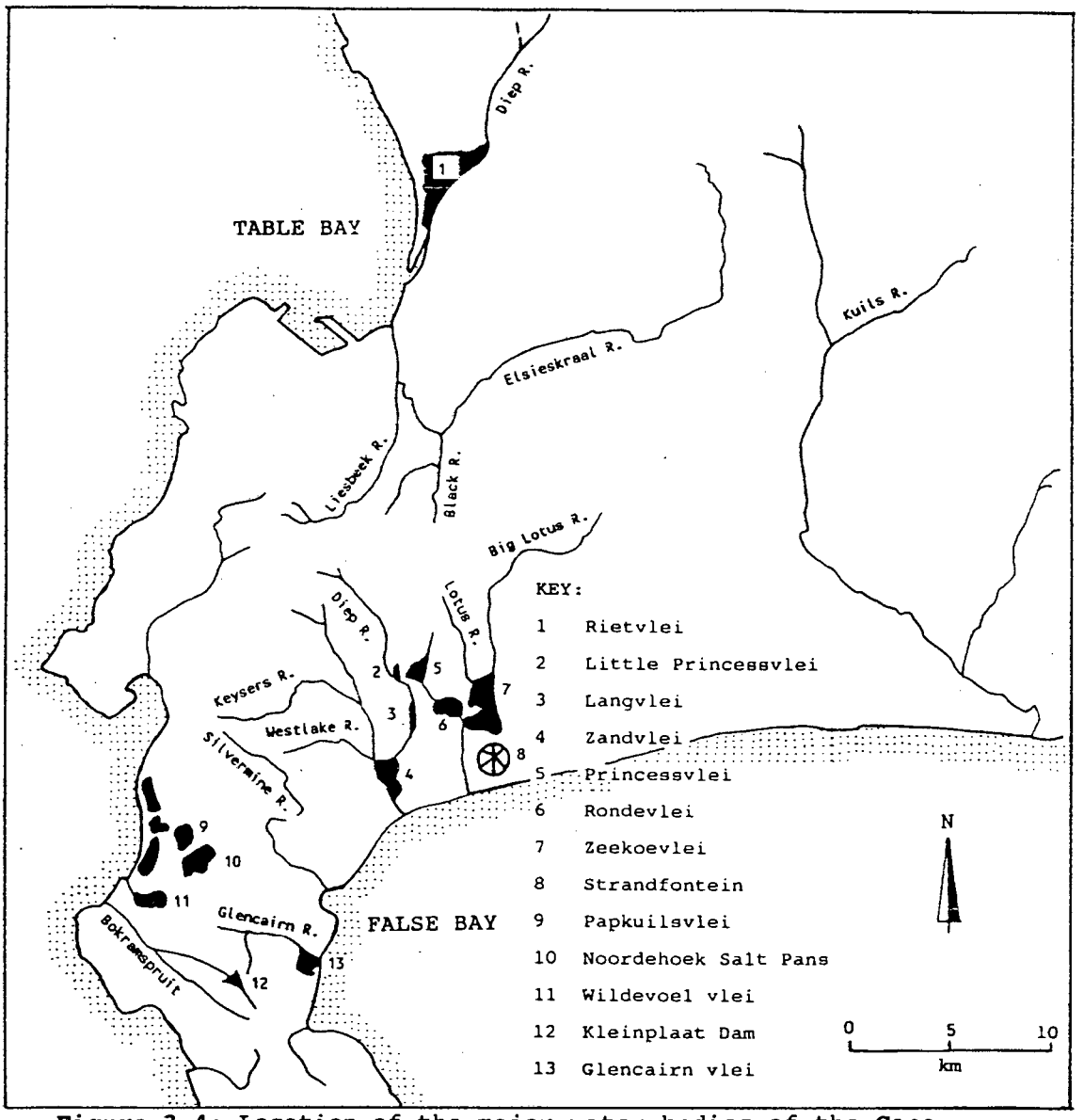



**Figure 3.4:** Location of the major water bodies of the Cape Peninsula.

**Rietvlei-Milnerton Lagoon**

(No.1 on figure 3.4)

This system lies in a 500km$^2$ basin 10km north-east of Cape Town. The Diep River rises in the Riebeek-Kasteel Mountains, drains the farmlands to the north of Cape Town and then flows through Rietvlei and into the lagoon (Day & King, 1980). The brackish, seasonal river, although small, used to be navigable. Today the river is silted and shallow due to agricultural development in the catchment (Grindley & Dudley, 1988).

Rietvlei is roughly triangular in shape, being 4km

wide and 2,0km wide (Fig. 3.5). It has an average depth of 2m, although the western basin is much deeper, having been dredged to allow for boating and other recreational activity (Grindley & Dudley, 1988). The northern, north-western and southern shores of the vlei are residential areas. The south-western shore is largely undeveloped and there is some Strandveld vegetation in this area. The eastern shore has an industrial area which includes a Wastewater Treatment Works, fertiliser factory and an oil refinery. The eutrophic characteristics of the vlei are derived from agricultural runoff and sewage effluent (Grindley & Dudley, 1988). The vlei mouth, which is a nature reserve, is surrounded by extensive *Phragmites australis* and *Typha* beds and supports a large water fowl population.

The lagoon is a seasonal blind estuary containing almost fresh water in winter, when the mouth is open, and hypersaline water in summer, after a sand-bar forms and closes the mouth (Day & King, 1980). When open, the lagoon is up to 1m deep and is tidal only as far as the vlei. Siltation is a problem in the lagoon, which has to be dredged occasionally.

**The Princessvlei-Rondevlei-Zeekoevlei System**

(Nos. 5-7 on figure 3.4)

This system of vleis is linked by a series of canals (Fig. 3.6). The Southfield Canal drains into Princessvlei, which discharges water into Rondevlei via the Italian Road canal. Rondevlei and Zeekoevlei used to be linked by a small canal on Rondevlei's eastern shore, but the connection has been diverted by a weir on Rondevlei's southern shore. Both vleis now discharge into the Zeekoe River which is canalised for part of its length (Fig. 3.6). This river also receives effluent discharge from the maturation ponds of the Strandfontein Wastewater Treatment Works.

Princessvlei is the smallest vlei in this system, with an area of 29ha and maximum depth of 3m (Day & King,

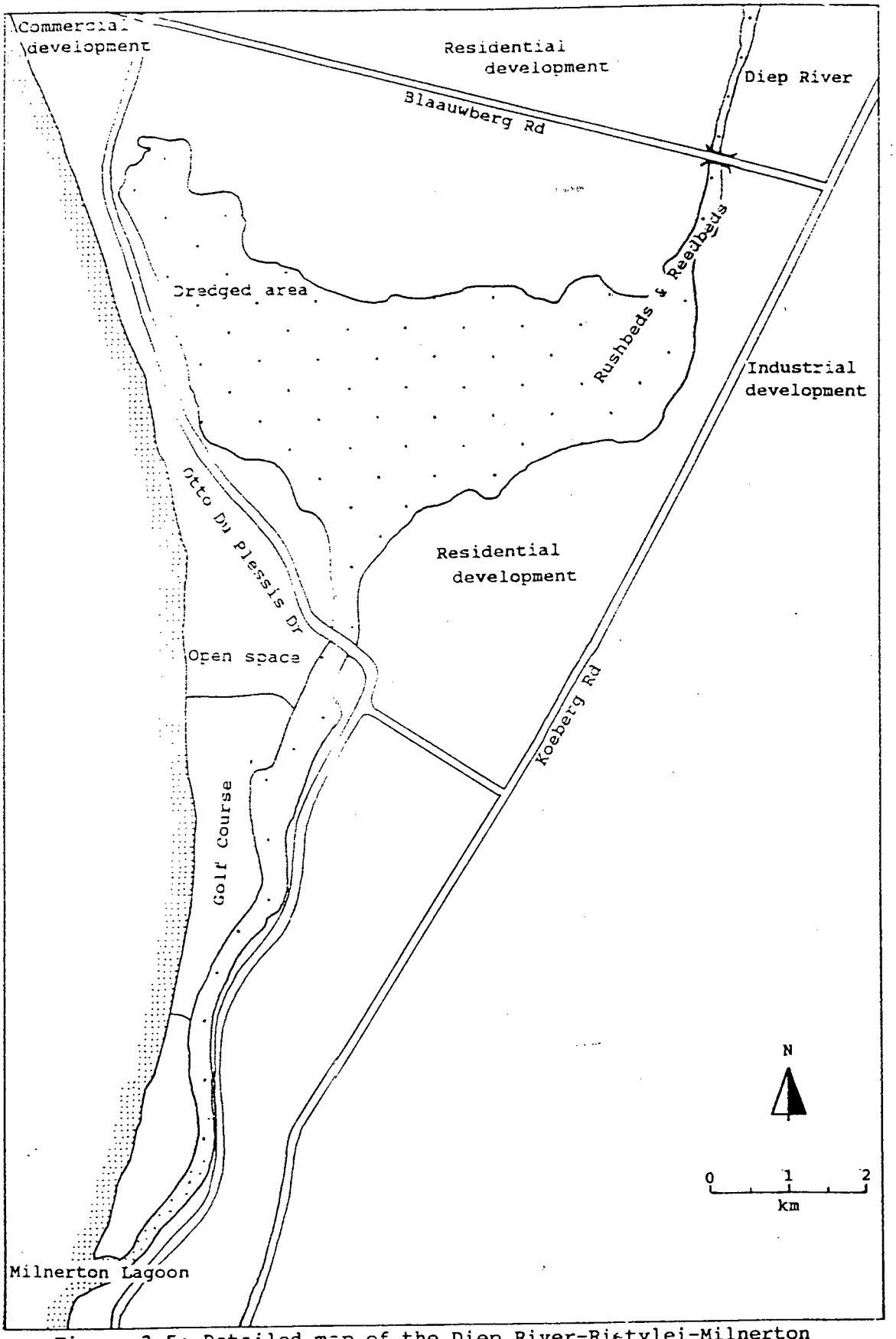



**Figure 3.5:** Detailed map of the Diep River-Rietvlei-Milnerton Lagoon system.

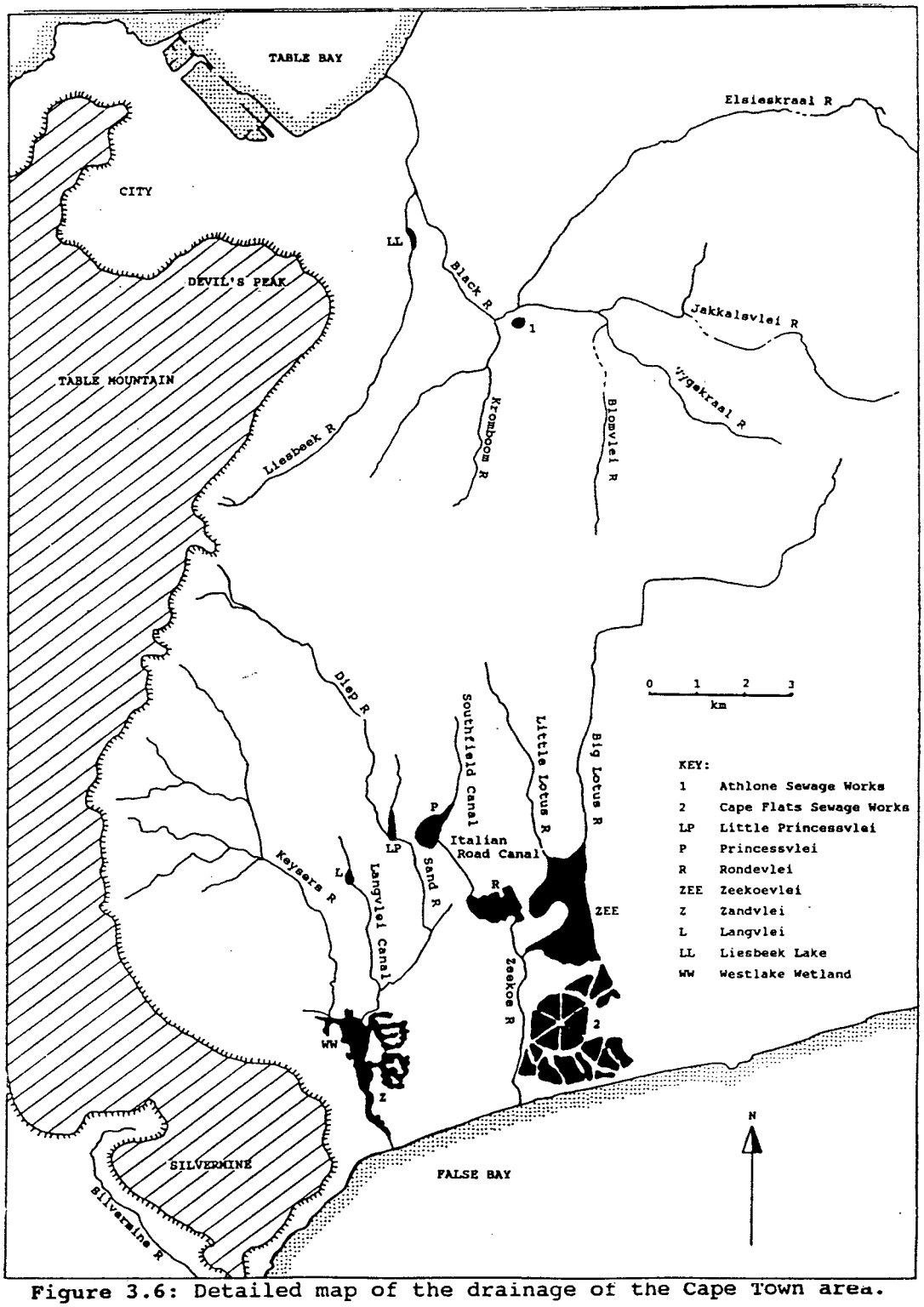



**Figure 3.6:** Detailed map of the drainage of the Cape Town area.

1980). The vlei is fed by the Southfield Canal, which drains an urban catchment of approximately 800ha, as well as a number of small stormwater pipes. Water depths are controlled by an outlet weir which has a crest height of 6.6m. The vlei is principally managed as a recreational area for boating and fishing, and to facilitate this, was dredged to an average depth of 1.9m during 1983 (Dick, 1983). This may be why waterlilies (*Nymphaea* spp.), common in the past (Stephens, 1929), are no longer present (Day & King, 1980; personal observation). The vlei shores are dominated by emergent species, particularly *Phragmites australis* and *Typha capensis*, although *Cyperus* spp. and *Scirpus* spp. are also common. Nutrient levels of the water are high (Dick, 1983), but have fallen since the vlei was dredged (Harding, 1991). Nitrate + nitrite concentrations ranged between 0.01 and 0.88mgN $l^{-1}$ between 1989 and 1990, while total soluble phosphorus varied between 0.01 and 0.16mgP $l^{-1}$ during the same period (Harding, 1991).

Rondevlei is a shallow-water wetland of 47.5ha. It has a catchment area of 1 492ha, which is fed by canal systems. These receive water from the high-density suburbs of Grassy Park and Retreat (Gardiner, 1988; Semmelink, 1990). Rondevlei used to be a seasonal vlei, and has dried up completely on several occasions (Middlemiss, 1974). However, the construction of the weir and increased runoff from the catchment has since resulted in reduced water level fluctuations. The vlei has had problems with a number of undesirable plant species including *Paspalum vaginatum*, which was successfully controlled by the introduction of *Hippopotamus amphibious*. More recently, *Typha* has encroached on sandbank areas. The vlei lies within the Rondevlei Bird Sanctuary which is an important water fowl breeding area (Middlemiss, 1974).

Zeekoevlei is the largest vlei in the study area and covers 256ha. It is 2 360m long, 1 560m wide at its widest point and has a mean depth of 1.9m (Rudnick,

1986). The vlei is fed by two rivers, the Big Lotus River and the Little Lotus River (Fig. 3.6). Both of them are canalised and are nutrient enriched, receiving seepage from surrounding septic tanks and the Strandfontein Wastewater Treatment Plant (Rudnick, 1986). Some chemical characteristics of Zeekoevlei and the Big and Little Lotus River are presented in Table 3.1. These have not changed appreciably since 1983 (Harding, 1991). Water level fluctuations in the vlei are restricted by a weir at the outflow, which has a major effect on the physical and biological characteristics of the vlei (Harding, 1991). There used to be extensive *Potamogeton pectinatus* beds in this vlei (Stephens, 1929), but these were deliberately removed during 1951 and have not reappeared since (Day & King, 1980). Instead, the vegetation is dominated by dense algal-cyanobacterial blooms (Rudnick, 1986; Harding, 1991). The littoral zone supports an extensive fringe of emergent vegetation which includes *Phragmites australis*, *Scirpus littoralis* and *Typha capensis* (personal observation). Zeekoevlei is managed as a recreational area with facilities for sailing, rowing, power boat racing and fishing. It also supports large breeding populations of water fowl.

**Table 3.1:** Range of chemical characteristics of Zeekoevlei, Big and Little Lotus Rivers recorded during 1989-1990 (from Harding, 1991). Cond. - Conductivity (mS $m^{-1}$); DO - Dissolved oxygen, TKN - Total (Kjeldahl) nitrogen, $NO_3$-N - nitrate, $NO_2$-N - nitrite, TIN - Total inorganic nitrogen, TP - Total phosphorus, TSP - Total soluble phosphorus, SRP- Soluble reactive phosphorus, ss - Suspended solids, all in mg $l^{-1}$.

| CHEMICAL VARIABLE | ZEEKOEVLEI | BIG LOTUS RIVER | LITTLE LOTUS RIVER |
|---|---|---|---|
| pH | 8.9-10.6 | | |
| Cond. | 93-202 | | |
| DO | 7.1-16.6 | | |
| TKN | 1.7-6.6 | 1.3-4.0 | 0.9-3.3 |
| $NO_3$-N | 0.03-0.38 | | |
| $NO_2$-N | 0.01-0.94 | | |
| TIN | | 1.10-9.10 | 0.61-3.30 |
| TP | 0.29-0.9 | 0.29-1.54 | 0.11-0.95 |
| TSP | 0.01-0.51 | 0.12-1.29 | 0.04-0.65 |
| SRP | 0.01-0.45 | 0.10-1.20 | 0.03-0.49 |
| ss | 14-153 | 4-35 | 5-70 |

**The Little Princessvlei-Langvlei-Zandvlei System.**
(Nos. 2-4 on figure 3.4)
Little Princessvlei is a small, artificial vlei on the Diep River (Fig. 3.6). It is fed by stormwater drains and flows into the Diep River (Day & King, 1980). It has a catchment area of 20km$^2$ and covers an area of 6ha (Town Planning Branch, 1988). The margins are steep, and deep water inhibits the development of submerged macrophyte beds. *Typha* grows around the vlei margins, particularly around the inflow and outflow points.

Langvlei is the smallest vlei in this system and covers approximately 2.5ha. It is fed by a small stream and drains into Zandvlei via the Langvlei Canal and the Sand River. This vlei used to be covered in *Eichornia crassipes* (Furness, 1979) and *Phragmites australis* (Day & King, 1980), but is now dominated by *Typha*.

Zandvlei is 2.5km long, 0.5km wide and up to 1.5m deep (Day & King, 1980), with a catchment area of 9 200ha (Darroch, 1988). It was once a true estuary, but was cut off from the sea by siltation during the early part of this century (Morant & Grindley, 1982). The connection to the sea was reestablished in 1929 when a canal was cut to prevent flooding inland (Stephens, 1929; Day & King, 1980). The vlei is fed by three rivers (Fig. 3.6). The Diep River and Keysers River are seasonal streams originating on the eastern slopes of Table Mountain. They drain industrial, suburban and agricultural areas. The Westlake River drains the western side of the catchment, a residential and agricultural area. These two rivers enter the vlei via an extensive marsh area, Westlake Wetland, colonised primarily by *Phragmites australis*, although *Typha capensis*, *Scirpus littoralis* and *S. maritimus* are also common (Azorin, 1988). This area is a bird sanctuary. The salinity of vlei waters rises during the summer months when the mouth is closed, and vegetation in the vlei itself is restricted to species tolerant of these extremes (*Ruppia marotoma*,

*Potamogeton pectinatus* and *Phragmites australis* - Muir, 1974; Shelton, 1975). Eutrophication, associated with catchment development and the construction of a marina on the vlei's eastern bank, has resulted in the rapid growth of these species. They now have to be mechanically removed at regular intervals (Day & King, 1980).

**The Fish Hoek Bay Vleis**

(No. 13 on figure 3.4)

The Silvermine vlei is a small seasonally flooded wetland lying approximately 1km from the mouth of the Silvermine River. The river drains an area of 2 106ha, rising on the southern slopes of Table Mountains with its mouth in the north-eastern corner of Fish Hoek Bay (Fig. 3.7). Flooding, siltation and pollution do not appear to be problems in this vlei (Heinecken, 1982). *Phragmites australis*, *Typha* and *Scirpus* spp. dominate the wetland.

Glencairn Vlei is a relatively large but seasonal wetland close to the mouth of the Glencairn River. There appears to be no information on its history, development or limnology. Similarly, Klawer Vlei has received no attention. It is a very small (approximately 1.2ha), seasonally inundated wetland which develops in the Dido Valley during winter. A similar, but more permanent wetland was found below the spillway of the Kleinplaat Dam, which is close to Dido Valley (Fig. 3.4). It is assumed that this wetland has developed as a result of the dam being built.

**Papkiulsvlei-Wildevoelvlei-Noordehoek Salt Pans System**

(Nos. 9-11 on Figure 3.4)

This is an extensive wetland system lying in the Noordehoek basin, draining a combined catchment area of 424km$^2$, most of which is agricultural (Heinecken, 1985). Undeveloped areas are vegetated by Coastal Fynbos, which has been invaded by alien *Acacia* spp., while the dunes are colonised by natural dune scrub.

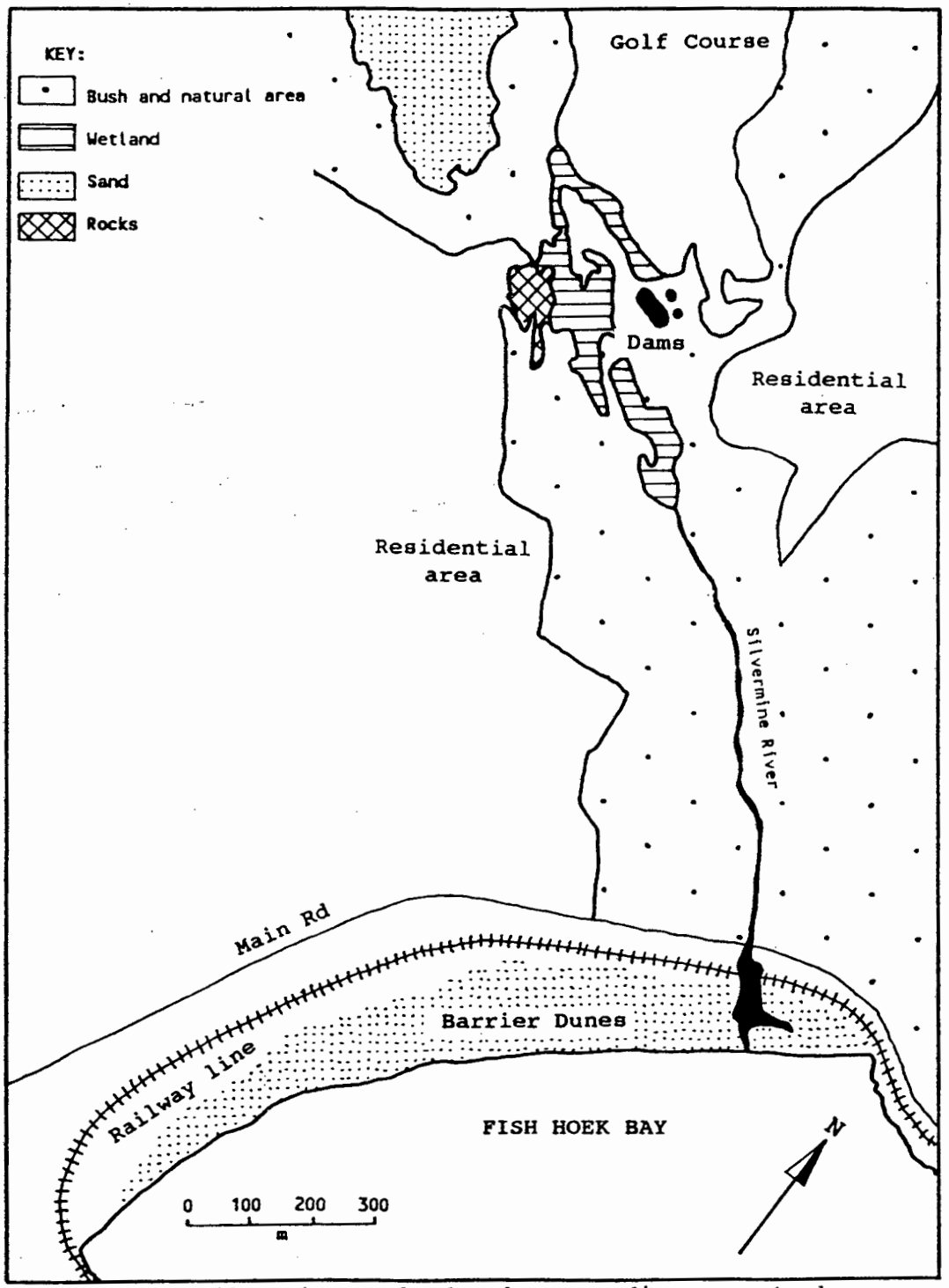



**Figure 3.7:** Silvermine wetland and surrounding area (redrawn from Heinecken, 1982).

The wetlands have formed in the poorly drained low lying areas of the basin which has only one well defined water course (the Goeiehoop River). Three major systems, interconnected by the high water table of the area, are recognised: the three large Salt pans which lie to the east of Papkuilsvlei, and the two Wildevoelvleis, which open into the sea via an outlet channel and spring-tide overwash lagoon (Fig. 3.8). The vleis used to be seasonal, but inflow to Wildevoelvlei from the wastewater treatment works now supplements summer flow. There are several smaller temporary wetland systems in the area, notably between the Sun Valley residential area and the Salt pans.

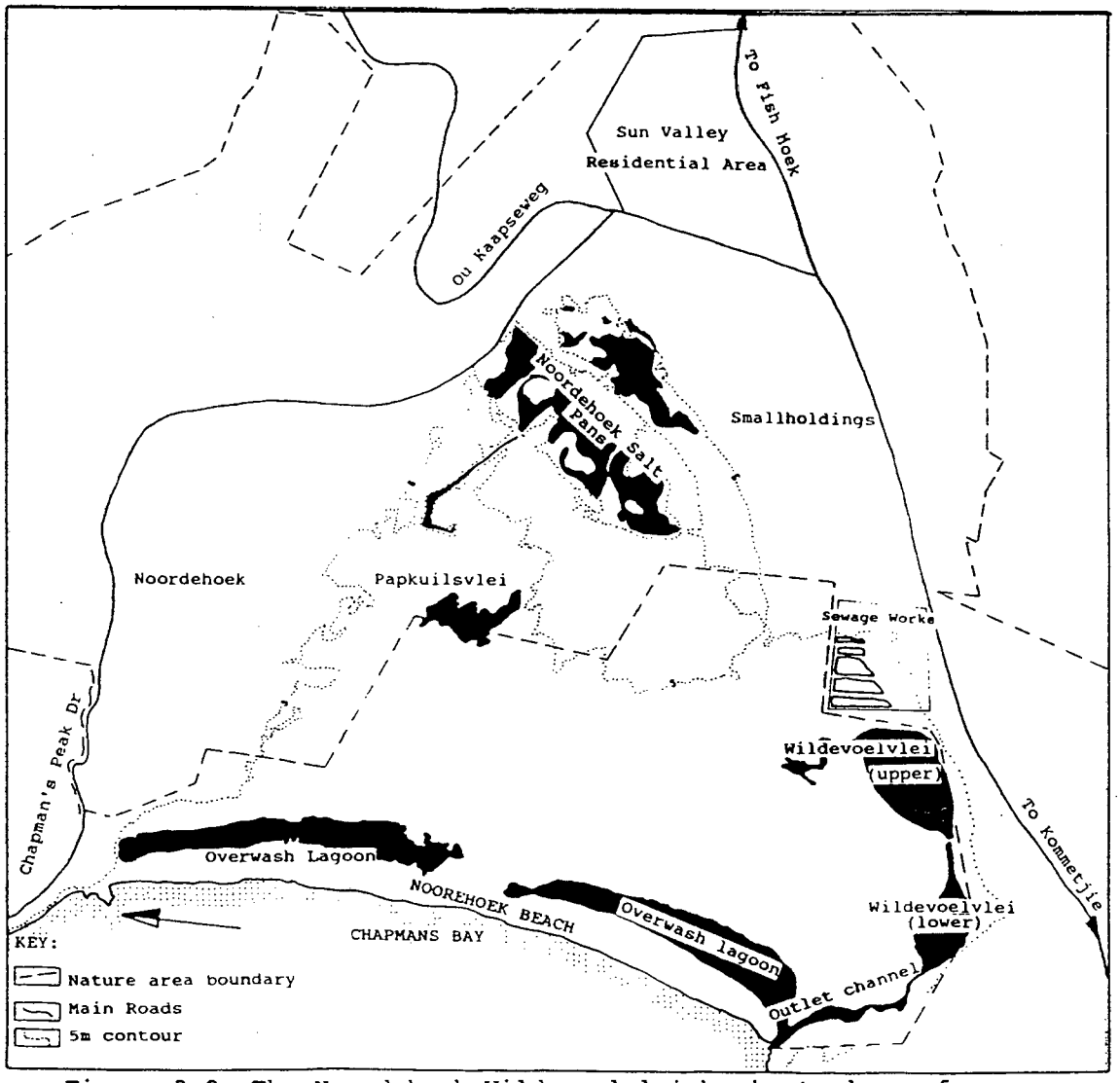



**Figure 3.8:** The Noordehoek-Wildevoelvlei basin (redrawn from Heinecken, 1985).

Effluent from the wastewater treatment works has increased nutrient levels and reduced seasonal water-

level fluctuations of the other vleis (Heinecken, 1982). Their salinity has also fallen and this has enabled *Typha*, which dominates Papkuilsvlei, to become established in the Salt Pans. These are, however, still dominated by *Phragmites australis*, *Scirpus maritimus* and *Juncus krausii* (Heinecken, 1985). The two pools of Wildevoelvlei have no fringing vegetation, but open water areas are dominated by extensive beds of *Potamogeton pectinatus*. There are also large stands of *Juncus krausii* in seepage areas around the outflow channel and lagoon (Heinecken, 1985).

**Rivers**

(Fig. 3.6)

The main river systems in the study area are the Kuils River in the east, and the central Black River system. Smaller rivers include the Liesbeek River which rises on the eastern side of Table Mountain and flows into the Black River; the Silvermine river which drains the western slope of the Back Table and enters the sea in the north-eastern corner of Fish Hoek Bay; the Hout Bay river; the Westlake, Keysers and Sand Rivers which drain the south-western part of the Cape Flats; and the Little- and Big-Lotus Rivers which supply Zeekoevlei.

**The Kuils River**

The Kuils river is 25km long and has a catchment of 154km$^2$ (Day & King, 1980; Wessels, 1981). The catchment is covered by Strandveld which has been invaded by *Acacia* spp. The river used to be seasonal, but has become strongly perennial due to receiving the outflow from the Bellville and Kuils River Wastewater Treatment Works, as well as increased runoff associated with the development of its catchment (Day & King, 1980). As a result the wetland has become a permanent feature of the lower reaches, and winter flooding has become a problem in the developed areas around the river (Fig. 3.9). Suggestions to control flooding have included dredging the river to prevent

overflow, and raising the level of adjacent land to prevent ground-water seepage (Brand, 1983). These measures will destroy the perennial wetland system and are likely to shift the problem of flooding to areas above and below treated areas. The wetland margins are dominated by *Typha capensis* and *Phragmites australis*. *Potamogeton pectinatus, Myriophyllum aquaticum, Eichornia crassipes, Nasturtium officinale* and *Rumex* spp. are present in the river and open water areas (personal observation). These plants probably act as a natural water purification system as water quality in the vlei is good (Brand, 1983).

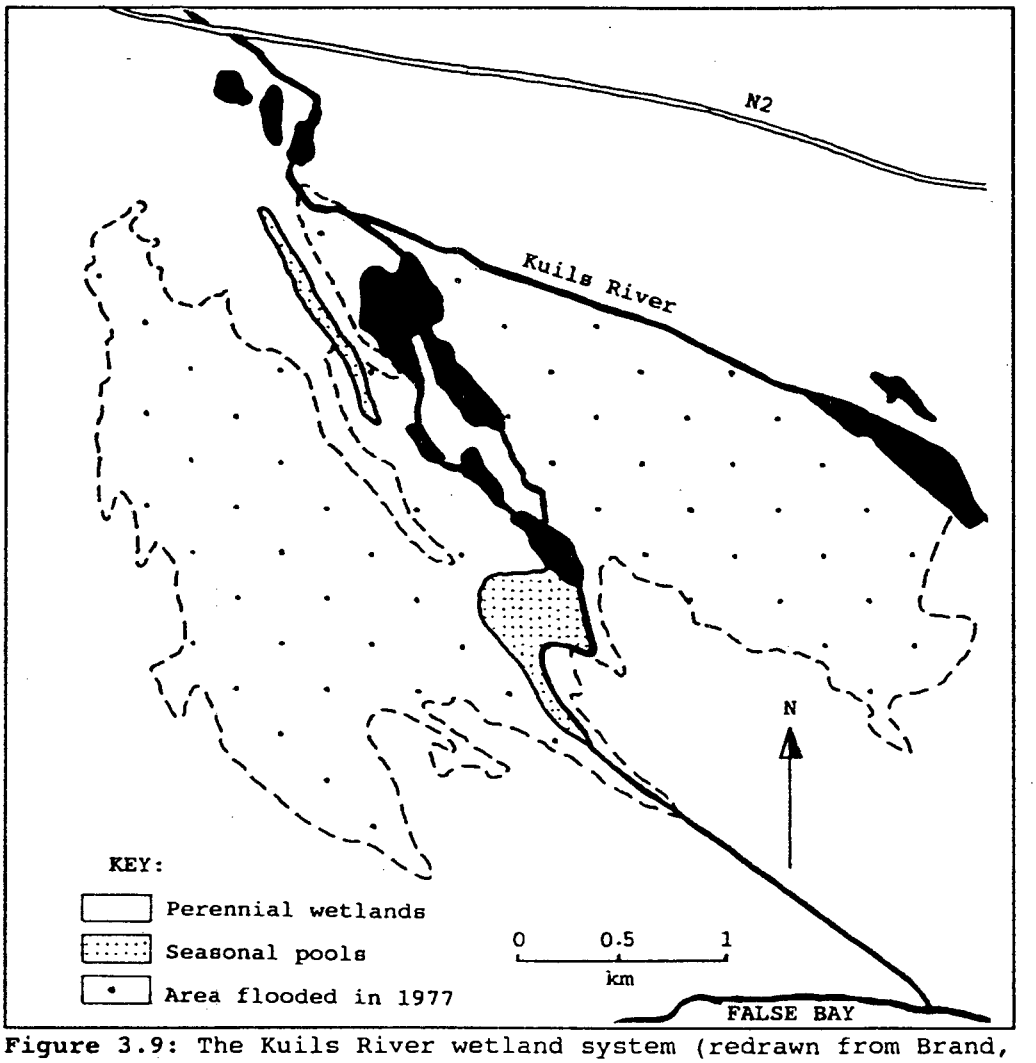



**Figure 3.9:** The Kuils River wetland system (redrawn from Brand, 1983).

**The Black River System**

The Black and Kromboom rivers join the Vygekraal and Elsieskraal rivers just below the Athlone Wastewater Treatment Works (Fig. 3.6). The system is then joined

by the Liesbeek River before entering the Salt River Canal which empties into Table Bay. A large proportion of the system is canalised or enclosed in storm water drains (Fig. 3.6), preventing the redevelopment of extensive temporary wetlands along the rivers during periods when the water table rises. Remnants of wetlands appear as seepage areas in uncanalised sections and as emergent macrophyte beds along the canals (personal observation). The quality of water in rivers entering the complex varies, but below the Athlone Wastewater Treatment Works the river is organically polluted (Table 3.2). Algal blooms are common and there are extensive submerged macrophyte beds (*Myriophyllum aquaticum* and *Potamogeton pectinatus*) in the lower reaches.

**TABLE 3.2:** Water quality in the Black River Complex (from Morrison, 1982). Cond. - electrical conductivity (mS $m^{-1}$); DO - dissolved oxygen, $NH_3$-N - ammonia concentration, $NO_3$-N - nitrate concentration, TP - total phosphorus and ss - suspended solids, all in mg $l^{-1}$.

| | VYEKRAAL | ELSIES KRAAL | BLACK R RAAPEN -BERG | BLACK R MAIT-LAND |
|---|---|---|---|---|
| pH | 95-140 | 7.3-9.0 | 7.1-8.1 | 7.1-8.0 |
| Cond. | 16-55 | 78-190 | 65-140 | 44-130 |
| DO | 1.1-4.6 | 9.0->20 | 2.1-7.4 | 0.9-6.3 |
| $NH_3$-N | 2.88-29.1 | 0.03-0.2 | 2.0-26.7 | 3.02-26.2 |
| $NO_3$-N | 1.4-7.0 | 0.1-12.5 | 1.2-6.8 | 0.4-4.2 |
| TP | 2.1-10 | 0.13-6.6 | 1.8-13 | 1.3-14 |
| ss | 14-220 | 12-140 | 9-140 | 4-49 |

| | LIESBEEK RIVER | BLACK RIVER MOUTH | JAKKELS -VLEI | LANGA CANAL |
|---|---|---|---|---|
| pH | 6.6-8.0 | 7.4-8.2 | 7.2-8.4 | 6.2-8.2 |
| Cond. | 10-28 | 50-810 | 31-160 | 50-190 |
| DO | 1.5-9.4 | 2.9-12.0 | 4.5-9.1 | 1.4-11.0 |
| $NH_3$-N | 0.05-0.4 | 0.09-25.3 | 0.16-4.3 | 0.04-1.8 |
| $NO_3$-N | <0.01-0.6 | 0.4-2.5 | 0.3-8.8 | 0.08-5.9 |
| TP | <0.01-0.3 | 0.56-13 | 0.96-11 | 0.15-4.8 |
| ss | 4-16 | 8-46 | 5-27 | 31-130 |

## MATERIALS AND METHODS

A survey to establish the present distribution of rushbeds was the first priority in this study of alleged encroachment by *Typha*. A total of 25 permanent wetlands in the study area were visited in late summer and in mid-winter. On each visit physical, chemical and floristic variables were measured.

Water samples were collected in a 10l bucket from just below the water surface close to the inner edge of the rushbeds, taking care to not disturb sediments in the area being sampled. Salinity, pH and electrical conductivity were measured immediately, using respectively a salinometer, a Hellige Lilliput pH meter (model 750/750) and a Crison 523 electrical conductivity meter with built-in temperature compensation. The pH meter was calibrated at pH 4 and 7 before use on every occasion. Subsamples (150ml) were immediately filtered through Whatman G/FF glass-fibre filters (0.45um pore size) using a hand-operated vacuum pump before they were frozen on dry ice for subsequent nutrient analysis. Samples were stored in acid-washed plastic ($NO_3$-N, $NO_2$-N and $PO_4$-P) or glass ($NH_4$-N) bottles, in a deep-freeze, for no more than four months prior to analysis. Nitrate, ammonium and soluble reactive phosphorus were measured by automated analysis (Technicon Auto-Analyser) using the methods recommended by Mostert (1983).

Soil samples were collected using a stainless steel corer (5cm diameter, 30cm depth) pushed, by hand, into the sediments. The depths of different layers (litter, organic, sand) were measured using a ruler marked in millimetres which was laid next to the intact core. The litter layer was removed before the soil sample was sealed in plastic and stored on ice until taken to the laboratory. Subsamples were collected after the sample was well mixed. These were suspended in distilled water (in a 5:1 ratio of water

to soil), stirred and allowed to settle for 20mins, before pH and electrical conductivity measurements were made (Allen *et al.*, 1986). Other subsamples were oven dried to constant weight at 60°C for measurement of soil moisture. Air dried samples (100g) were mechanically shaken through a graduated series of six sieves (range of 1 - 5phi) for 10mins. Each fraction was then weighed and recorded as a percentage of the sample weight. This method did not separate clay and silt particles, but gave an indication of soil coarseness.

Percentage species cover was visually estimated using a $1m^2$ quadrat, with a removable side and marked in quarters to make estimation more accurate. Standing stocks were measured using harvest methods to measure the live aboveground biomass of each species (Moore & Chapman, 1986). All live plant material was clipped at ground level, sorted by species, weighed to determine the fresh weight of each fraction and then subsampled (3 replicates per species) for the determination of dry weight. Large emergent species were chopped into 20cm lengths to facilitate subsampling. Subsamples were taken to the laboratory, oven dried to constant weight at 60°C, and weighed to determine dry mass.

The size, density and average shoot height of rushbeds in small temporary wetlands (ditches, canals, seepage areas) were also noted. Information from other wetland reports was included when compiling the data presented here. Nevertheless, the list of wetlands where *Typha* is found on the Cape Flats is not exhaustive, as it was impossible to visit every stand of *Typha* in the area.

Detailed vegetation maps for some vleis were drawn from recent aerial photographs (1987; Cape Town City Council City Planning Department), and were verified by ground survey (Azorin, 1988). Assuming that different species appeared as different colour and/or

textures on the aerial photographs, maps were drawn showing the boundaries between vegetation types. Approximately half of these areas were then located at each site, and the species composition of the stand determined as percentage cover of each species within twenty $1m^2$ quadrats. In the majority of cases, stands were monospecific and, therefore, easy to recognise from aerial photographs.

Photographs suitable for vegetation mapping (at least 1:50 000 scale - Weisser & Standler, 1983) were not available, so it was impossible to investigate the development and spread of beds with this technique. Instead, local records, plant collections (including herbarium specimens) and anecdotal commentaries were consulted in order to estimate when the rushbeds first appeared, and how quickly they had spread.

A more precise measure of the rate of stand encroachment was made at Rondevlei using grid mapping techniques (Ham *et al.*, 1982). Permanent stakes were positioned at 5m-intervals along a 20m strip of shoreline which had been recently cleared. The edge of the bed within each $5m^2$ quadrat was mapped in July 1987 and again at six monthly intervals until June 1989.

In order to ensure objective assessment of the "weediness" of *Typha*, surveys of public opinion and of the scientific literature were conducted. The public survey involved a questionnaire offered to 60 householders from the Zeekoevlei Peninsula, who have had to deal with the plant (see Appendix I; this chapter). Those householders not familiar with *Typha* were shown how to identify it before they completed the form.

# RESULTS AND DISCUSSION

## WETLAND SURVEY

The results of the survey, together with data extracted from Grindley (1988), Morant & Grindley (1982), Silberbauer & King (1991) and Azorin (1988), are presented in Table 3.3 which summarises some of the water, soil and floristic characteristics of some Cape wetlands. Where possible, data regarding water depth and soil and water chemistry are presented as ranges, although in most instances these figures are derived from only two samples (one winter and one summer). Soil moisture measurements were grouped into two categories according to the summer (dry period) measurement. "Wet" indicates that soil moisture was >20%, while soil moisture <20% is described as "dry". Soil moisture was described as "constant" if it was similar (within 5%) at both visits, or "seasonal" if it varied more than 5% between summer and winter. In this way a wetland where soil moisture was less than 20% in summer, but rose at least 5% during winter is described as "seasonally dry", while if soil moisture was above 20% in summer and it increased significantly during winter, the wetland is described as "seasonally wet". The shape of the wetland bank is described as gentle if the slope was less than 60°, steep if it was greater the 60°. The plant community is described according to the dominant emergent species (either *Typha* or *Phragmites australis*), and its density.

The wetland survey covered a wide variety of habitats: from stagnant pools, to strongly flowing streams; from deep standing water, to seasonally damp depressions; wetlands with steep or gentle bank slopes, and those with gravel, sand or silt sediments. Water salinity varied from fresh to brackish, while pH ranged from 4.0 to 9.4. Most of the wetlands visited had high nutrient (nitrogen and phosphorus) concentrations (Table 3.3).

**Table 3.3:** Summary of the results of the wetland survey conducted. Reference numbers are as follows: 1 - Grindley, 1988; 2 - Morant & Grindley, 1982; 3 - Silberbauer & King, 1991; 4 - Azorin (1988). Soil moisture: wet - >20% in summer; dry <20% in summer. Duration - period when soil moisture >20%. Bank slope: gentle - <60°. Plant community: T - tall, dense stands of *Typha*; t - short, sparse stands of *Typha*; P - *Phragmites*; NE - no emergent vegetation. Other details are given in the text.

| SITE | WATER DEPTH (cm) | FLOW | pH | CONDUC-TIVITY mS m$^{-1}$ | SALI-NITY ‰ | WATER $PO_4$-P mg l$^{-1}$ | WATER $NO_3$-N mg l$^{-1}$ | SOIL TYPE | SOIL MOISTURE: SUMMER | DURATION | SOIL CONDUCT-IVITY mS m$^{-1}$ | SOIL pH | BANK SLOPE | PLANT COMMUNITY | REFER-ENCE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cape Corp | 0-45 | no | - | 1042 | - | - | - | sand | wet | constant | - | - | gentle | T | 3 |
| Diep River | 0 | yes | - | 124 | - | - | - | sand | wet | constant | - | - | gentle | T | |
| Glencairn wetland | 0-80 | no | - | 98 | - | 0.02 | 0.03 | sand | wet | constant | 44 | 9.9 | gentle | T | |
| Kenilworth Racecourse | | no | 4 | 23 | 0 | <0.001 | <0.01 | sand | wet | constant | - | - | gentle | T | |
| Kleinplaat dam | 0-15 | yes | 5 | 17 | 0 | - | - | silt | wet | constant | - | - | gentle | T | |
| Kuils River | 1 | yes | 9.3-9.2 | 94-1223 | 0 | <0.001-5.05 | 0.19-0.44 | sand | wet | constant | - | - | gentle | T | |
| Langvlei | 0-65 | no | 7.2 | - | 0 | - | - | silt | wet | constant | - | 7.2 | gentle | T | |
| L. Princessvlei | 160 | no | 6.5 | - | 0 | - | - | silt | wet | constant | - | 6.2 | gentle | T | |
| Princessvlei | 0-75 | yes | 6.2 | 69 | 0 | 0.16-0.34 | 0.01-0.02 | sand | wet | constant | 14.1-37.1 | 5.4-6.2 | gentle | T | |
| Rondevlei | 15-130 | no | 6.5-9.7 | 111-417 | 0 | - | - | sand | wet | constant | - | - | gentle | T | |
| Strandfontein Sewage | 0-70 | no | 8.4 | 310 | 0 | - | - | sand | wet | constant | - | - | gentle | T | |
| Sun Valley | 0-30 | no | - | - | 0 | 0.03 | 0.16 | silt | wet | constant | - | - | gentle | T | |
| Zeekoevlei | 0-60 | no | 7.4-9.4 | 104-211 | 0 | 0.16 | - | sand | wet | constant | 55.2-280 | 7.5-9.1 | gentle | T | |
| Zandvlei | 80-150 | no | 6.8 | - | - | - | - | sand | wet | constant | - | - | gentle | T | |
| Silvermine wetland | 1 | no | 7.5 | 106 | 0 | 0.01 | 0.01 | sand | wet | seasonal | 63.4 | 8.5 | gentle | t | |
| Klawer vlei | 2-25 | yes | 4-9 | 82-108 | 0 | 0.01-0.12 | 0.08-0.19 | gravel | wet | seasonal | 616 | 7.8 | gentle | t | |
| Orange St reservoir | 5 | no | 8.4 | 310 | 0 | - | - | sand | dry | seasonal | 234 | 6.0 | gentle | t | |
| Rondevlei (b) | 0-15 | no | 6.5-9.2 | 111-417 | 0 | - | - | sand | dry | seasonal | - | - | gentle | t | |
| Zeekoevlei (b) | 0-60 | no | 7.4-9.4 | 104-211 | 0 | 0.17 | - | sand | dry | seasonal | 176-271 | 7.5-8.7 | gentle | t | |
| Lotus River | 0-55 | yes | 8.2 | 115 | 0 | - | - | sand | wet | seasonal | - | 7.5-8.2 | gentle | t | |
| Milnerton ditch | 22 | no | 7.2 | 124 | 0 | - | - | gravel | dry | seasonal | - | - | gentle | t | |
| Noordehoek ditch | 0-23 | no | 8.5 | 3 | 0 | - | - | sand | dry | seasonal | - | - | gentle | t | |
| Westlake stream | 0-55 | no | 7.1 | 41 | 0 | - | 0.11 | sand | dry | seasonal | - | 6.5 | gentle | t | |
| Black river bank | 20-50 | no | 7.5-8.2 | 177-400 | 0 | 0.99 | 0.25 | silt | wet | constant | 429-2200 | 7.2-7.8 | gentle | T | |
| Black river (b) | 20-50 | no | 7.5-8.2 | 177-400 | 0 | 0.99 | 0.25 | silt | dry | constant | 429-2200 | 7.2-7.8 | gentle | P | |
| Rietvlei | 0-40 | no | 7.3 | 314 | 0 | 0.15 | 0.31 | silt | wet | constant | - | 1.8-8.0 | gentle | T | |
| Rietvlei (b) | 0-40 | no | 7.3 | 314 | 0 | 0.15 | 0.31 | silt | dry | constant | - | 1.8-8.0 | gentle | P | |
| Spaanschemat river | 34 | yes | 6.5 | 44 | 0 | 0.07 | 0.09 | sand | wet | constant | 14 | - | gentle | T | |
| Spaanschemat river (b) | 34 | yes | 6.5 | 44 | 0 | 0.07 | 0.09 | sand | dry | constant | 14 | - | gentle | P | |
| Hout Bay river | 0 | yes | 4.5-6.0 | - | 2 | <0.01 | <0.01-1.24 | sand | dry | constant | - | - | gentle | P | 1 |
| Keysers river | 0 | yes | - | - | 3 | - | - | sand | dry | constant | - | - | steep | P | |
| Noordehoek saltpan | 0-15 | no | 8.1 | 417 | 3 | 0.17 | <0.01 | sand | dry | seasonal | - | - | gentle | P | 3 |
| Silvermine wetland (b) | 0 | no | 7.5 | 106 | 0 | 0.01 | 0.01 | sand | dry | constant | 42.3 | 8.8 | gentle | P | |
| Westlake stream | - | yes | 5.8-8.5 | 43-189 | 0-11 | <0.01-0.56 | <0.01-1.24 | sand | dry | constant | - | - | gentle | P | 2 |
| Zandvlei | 80-150 | no | 6.8 | - | - | - | - | sand | wet | constant | - | - | gentle | T | 4 |
| L. Princessvlei (b) | 160 | no | 6.5 | - | 0 | - | - | sand | wet | constant | - | 6.2 | steep | NE | |
| Princessvlei | 220 | no | 6.2 | 68 | 0 | 0.15-0.34 | 0.01-0.02 | sand | wet | constant | 14.1-37.1 | 5.4-6.2 | steep | NE | |
| Silvermine river | 5 | yes | 6.5 | 24 | 0 | 0.01 | 0.01 | gravel | wet | constant | 1157 | 7.0 | gentle | NE | |
| Strandfontein (b) | 0-70 | no | 8.4 | 310 | 0 | - | - | sand | wet | constant | - | - | steep | NE | |
| Sun Valley (b) | 0-30 | yes | - | - | 0 | 0.02 | 0.16 | silt | wet | seasonal | - | - | steep | NE | |

*Typha* stands were found at most sites visited (Table 3.3). Exceptions included the head waters of many rivers, the acidic wetlands on the summit of Table Mountain, and most canalised water courses. Along the latter, however, *Typha* was established in adjacent damp areas, where canal beds had been broken, or where there had been sediment build up.

Although most wetlands contained *Typha*, the extent to which they were colonised varied widely. In some (e.g. Langvlei, Fig. 3.10) most of the wetland was covered by a single rushbed, while in others (e.g. Princessvlei, Fig. 3.11) small isolated beds were scattered around the shoreline. The size of all the stands appeared to be limited by two factors: wetland topography and water supply (Table 3.3). *Typha* shoots were confined to areas which were damp in summer (>20% soil moisture), but which were not flooded to more than 1.2m in winter. Within these areas rushes were absent where the banks were steeply sloped (e.g. along the margins of maturation ponds).

Rushbed development varied widely within the study area. Generally the most luxuriant growth (mean shoot height >2.0m; mean density >15shoots $m^{-2}$) was recorded in areas where shoots were growing in standing water of high nutrient concentration (Table 3.3). Very sparse stands (<4shoots $m^{-2}$) were recorded in areas, such as canal edges and roadside ditches, where the sediments were suitably damp to facilitate germination and seedling development, but which became dry in summer.

The species composition of emergent macrophyte communities was usually related to water supply (Table 3.3). Monospecific *Typha* stands occurred in constantly wet areas, with gently sloping banks. In wetlands where there was some flow, or where summer soil moisture was less than 20%, growth was less vigorous. At sites where *Typha* was found in close association with *Phragmites australis* (e.g. Rietvlei,

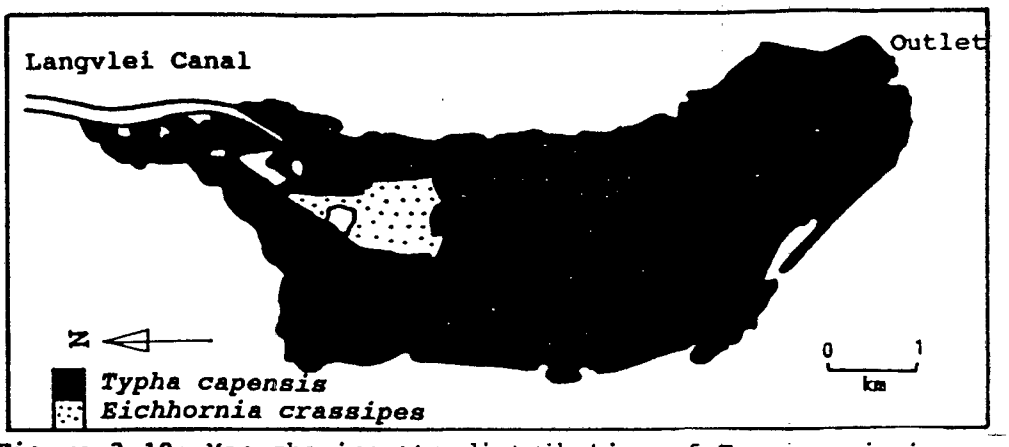



**Figure 3.10:** Map showing the distribution of *T. capensis* in Langvlei in 1987. Drawn from aerial photographs (City Plannners Department, Cape Town City Council).

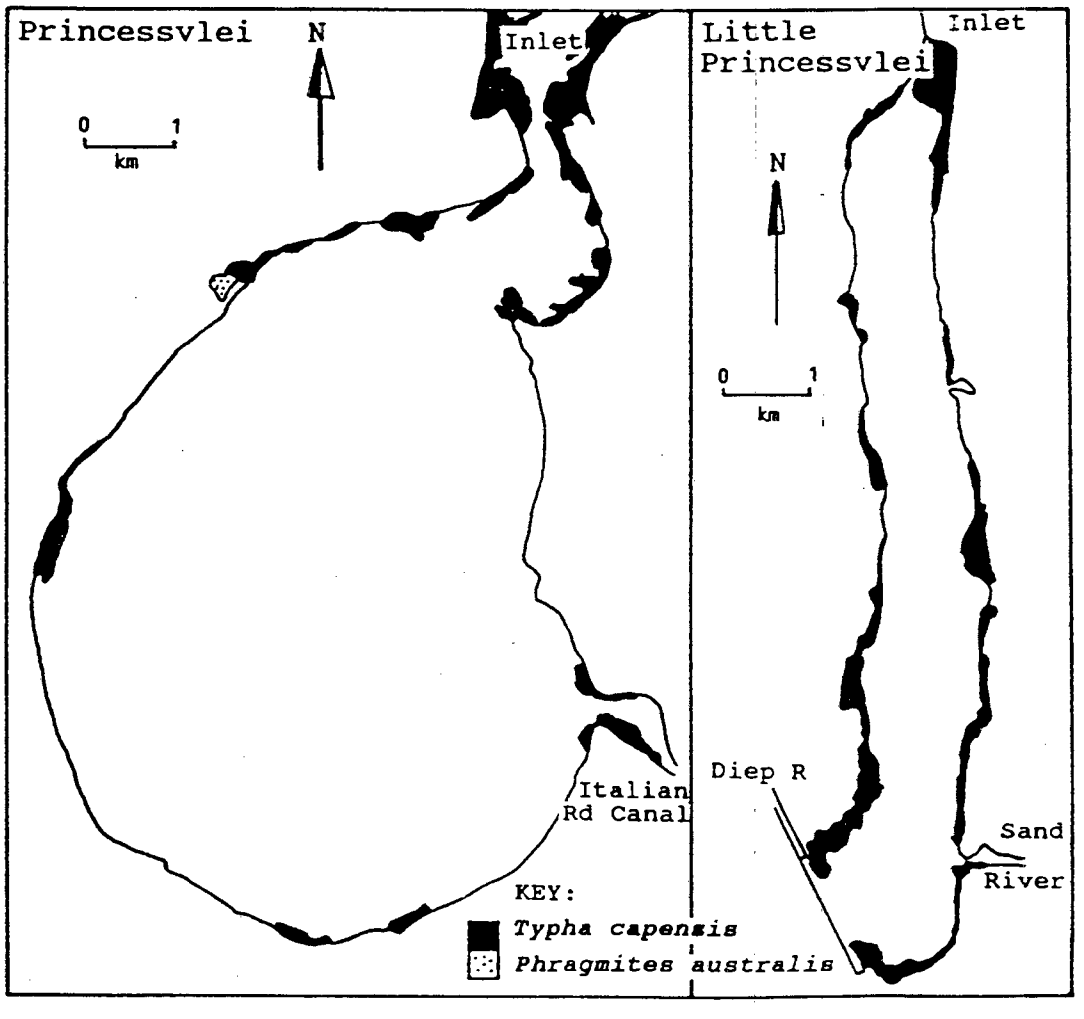



**Figure 3.11:** Maps showing the distribution of *T. capensis* in Little Princessvlei and Princessvlei in 1987. Drawn from Aerial Photographs (City Planners Department, Cape Town Cty Council).

Black River and Spaanschemat River), it occupied the wettest areas, while in wetlands where soil moisture was low, bank profiles steep and flow constant, or where salinity was above 1°/oo, *Phragmites* became the dominant emergent species. These relationships are discussed in greater detail later in the chapter, when describing general encroachment (page 79). The deep-water areas of permanently inundated wetlands (Rondevlei, Zeekoevlei, Rietvlei, Princessvlei and Little Princessvlei), were colonised by *Scirpus littoralis*.

*Typha* has a wide degree of environmental tolerance and can grow in a variety of substratum types, pH and oxygen concentrations (Agronomy Division, 1973; Finlayson *et al.*, 1983; Grace & Harrison, 1986). For this reason it is unlikely that these factors would influence rushbed distribution and encroachment. Nutrient levels play a more important role but, as most of the wetlands visited were nutrient enriched, it is difficult to evaluate the effect of eutrophication. Nevertheless, previous research has shown that dense *Typha* stands are associated with eutrophic systems (Dykyjova, 1978; Toivonen & Back, 1989; Toivonen & Nybom, 1989), so it is likely that they support the most luxuriant stands. Furthermore, the spread of emergent plants is generally associated with an increase in nutrient levels (Ksenofontova, 1989; Thompson & Shay, 1985), implicating eutrophication in rushbed encroachment.

## ENCROACHMENT

### Encroachment in Specific Wetlands

*Rondevlei*

The vegetation maps of Rondevlei, drawn between 1953 and 1987 (Fig. 3.12), show the dramatic spread of rushbeds around the wetland perimeter. During this period the area covered by *Typha* increased from 622 to 82 175m$^2$, increasing the proportion of the basin covered from 0.1 to 17.3% (Table 3.4). The

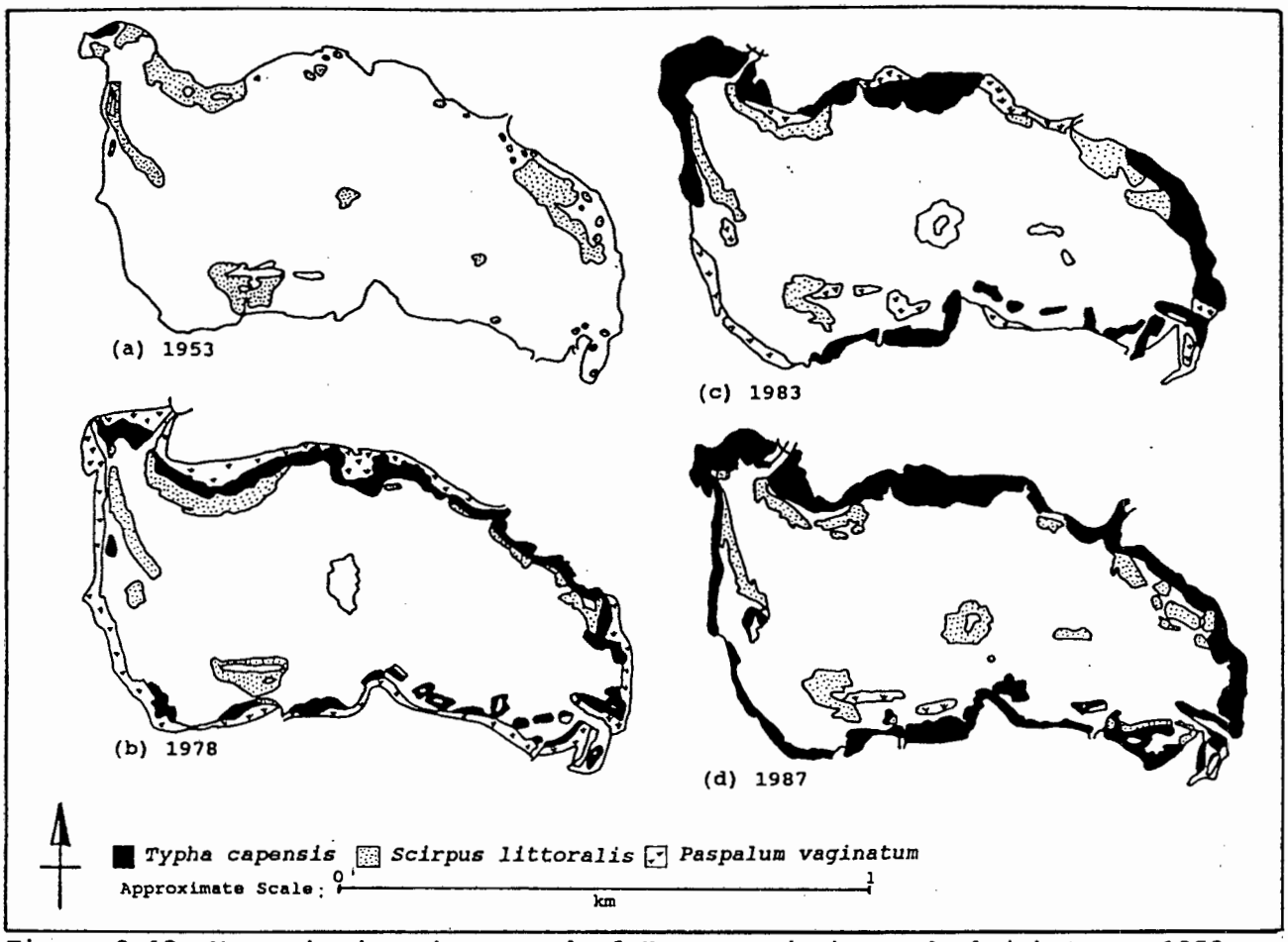



**Figure 3:12:** Maps showing the spread of *T. capensis* in Rondevlei between 1953 and 1987.

**Table 3.4:** Details of area and the distance of shoreline colonised by *Typha* beds at different times over the past 37 years, as calculated from Rondevlei vegetation maps. $A_o$ - lake area. $S_l$ - total shoreline.

| Date | Area Covered m2 | % of $A_o$ | Shoreline Colonised m | % of $S_l$ |
|---|---|---|---|---|
| 1953 | 622 | 0.1 | 97 | 1.5 |
| 1975 | 34 862 | 7.3 | 3 491 | 56.0 |
| 1983 | 60 511 | 12.7 | 3 782 | 60.7 |
| 1987 | 82 175 | 17.3 | 5 303 | 85.1 |

colonisation of the shoreline was even more dramatic: 1.5% in 1953; 85.1% in 1987.

The detailed mapping of the edge of a spreading *Typha* bed (Fig. 3.13) revealed that the bed was spreading along the shoreline at a monthly average of 0.96m, and into the vlei at 1.67m month$^{-1}$ (Table 3.5). Although these results cannot be applied to other systems, they do illustrate the plant's potential for rapid encroachment.

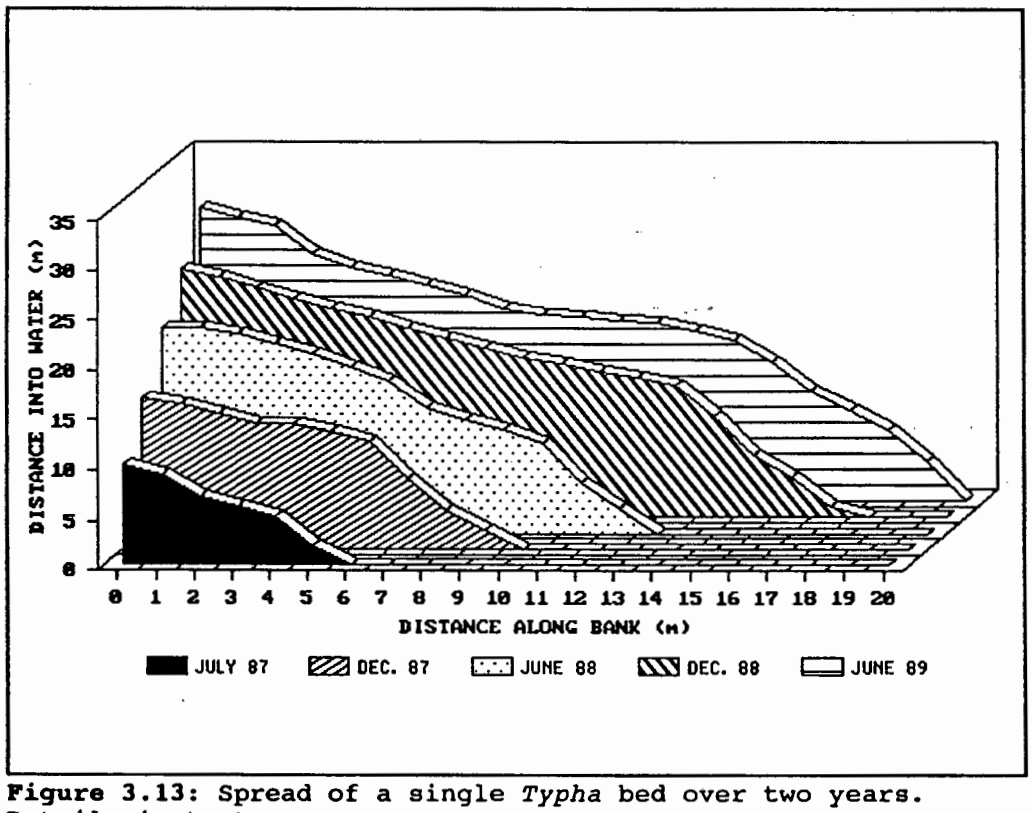



**Figure 3.13:** Spread of a single *Typha* bed over two years. Details in text.

**Table 3.5:** Details regarding the spread of a single *Typha* bed into and along Rondevlei, between July 1987 and June 1989.

| Date of Mapping | Spread along bank m month$^{-1}$ | Spread into vlei m month$^{-1}$ |
|---|---|---|
| July 1987 - Dec 1987 | 1.50 | 1.90 |
| Dec 1987 - June 1988 | 0.75 | 1.83 |
| June 1988 - Dec 1988 | 0.75 | 1.43 |
| Dec 1988 - June 1989 | 0.83 | 1.50 |
| Mean | 0.96 | 1.67 |
| Standard Error | 0.18 | 0.11 |

*Zeekoevlei*

In the early 1920s, the only littoral macrophyte species recorded in Zeekoevlei was a small stand of *Scirpus maritimus* growing in the wetland's northern arm (Stephens, 1929). In 1987, at least three-quarters of the littoral was colonised by dense *Typha* stands. It is unclear when *Typha* invaded the vlei, but photographs suggest that it was well established by 1968 (Davies, 1983).

Quick (1987) reported that the area covered by *Typha* in Zeekoevlei had increased by 84.7% between 1955 and 1983. Over the same period, the beds had encroached into the vlei at approximately 1.5m $yr^{-1}$.

In a similar investigation, rushbed area in Zeekoevlei was compared between 1968 and 1980 (Davies, 1983). Changes were not quantified, but the extent of emergent vegetation along the southern and north-eastern shorelines had increased. This change was primarily due to an increase in depth distribution (i.e. encroachment into, not around the vlei.)

*Langvlei*

In 1978 the entire vlei was covered by *Eichornia crassipes* (Furness, 1979), as was the case in the late 1920s (Stephens, 1929). When the vlei was photographed in 1987 most of the water hyacinth had been replaced by *Typha*, which covered 95% of the vlei (Fig. 3.10). Local residents say that *Typha* first appeared at the vlei in about 1980, suggesting that the rushes have colonised an area of approximately 6ha in 7 years.

*Rietvlei*

*Typha* and *Phragmites* have been present in the north-eastern corner of the vlei since at least 1960 (Mr. D. Brook, Milnerton Municipality, Milnerton pers. comm.). As Stephens (1929) did not record any emergent macrophytes here, it is assumed that *Typha* invaded the wetland between 1920 and 1960. Its distribution was

relatively stable until the early 1970s, but since then, the rushbeds have spread to cover approximately 60ha. This has been attributed to the development of sand banks at the mouth of the Diep River, enhanced by the nutrients supplied both by the agricultural catchment and by effluent discharge and seepage from the adjacent Wastewater Treatment Works (Grindley & Dudley, 1988).

**General Encroachment**

A literature search was used to identify variables which have been implicated in reported encroachment problems elsewhere in the world (Manning & Saunders, 1975; Weisser, 1979; Weisser & Howard-Williams, 1982; Beare & Jedler, 1987). These include:

1. increased water depth;
2. constant water level or a reduction in water level fluctuations;
3. decrease in water movement;
4. high nutrient levels or an increase in nutrient supply, particularly of nitrogen and phosphorus;
5. saucer-shaped littoral or reduction in shoreline slope, and
6. decrease in water or soil salinity.

Using management records and previous reports on Cape vleis the effect of these variables at each vlei was assessed. Results are summarised in Table 3.6 which groups wetlands with *Typha* stands according to whether or not the stands are spreading. Water supply, which determines water depth as well as water-level fluctuations depending on whether or not flow is seasonal, is described as increasing or constant. Seasonal water-level fluctuations were reduced if inflow had become less seasonal or if outflow had been reduced e.g. by the installation of a weir. The magnitude of water level fluctuation is described as high if summer drawdown exposed even the fringes of the *Typha* stand, or low if stand fringes remained

**Table 3.6:** Separation of wetlands where *Typha* is spreading from those where its distribution is stable. Water supply (WS): I - increased, C - constant. Seasonal water level fluctuation (F): R - reduced, C - constant, H - high, L - low. Flow (Fl): W - winter only, N - none, H - high, L - low. Nutrient status (NS): E - eutrophic, M - mesotrophic. Bank Slope (S): G - gentle, S - steep. Salinity (Sa) C - constant; D - decreased. Littoral cover (LC): Cl - cleared; D - sand banks created by drawdown; U - unchanged.

| WETLAND | WS | F | Fl | NS | S | Sa | LC |
|---|---|---|---|---|---|---|---|
| **PRESENT AND SPREADING:** | | | | | | | |
| Cape Corp | I | R | LW | E | G | C | U |
| Kuils River | I | R | LW | E | G | C | U |
| Langvlei | I | C | N | E | G | C | U |
| Rondevlei | I | R | N | E | G | C | D |
| Papkuilsvlei | I | R | N | M | G | C | U |
| Noordehoek Ditch | I | R | N | M | G | C | Cl |
| Rietvlei | I | R | LW | E | G | C | U |
| Sunvalley Ditch | I | R | LW | E | G | C | Cl |
| Zeekoevlei | I | R | N | E | G | C | D |
| Westlake Stream | I | R | LW | E | G | ?D | U |
| Noordehoek Salt Pan | I | R | N | E | G | D | U |
| **PRESENT BUT STABLE:** | | | | | | | |
| Diep River | I | H | H | E | S | C | U |
| Glencairn | C | H | HW | M | S | C | U |
| Kleinplaat Dam | C | C | H | M | S | C | U |
| Little Princessvlei | I | L | N | E | S | C | U |
| Princessvlei | I | L | N | E | S | C | U |
| Silvermine wetland | C | H | N | M | G | C | U |
| Strandfontein | C | L | N | E | S | C | U |
| Zandvlei | I | H | N | E | G | ?D | U |
| Dido Valley | C | H | H | M | S | C | U |
| Orange Street | C | H | N | M | G | G | U |
| Lotus River | I | L | H | E | S | C | U |
| Milnerton Ditch | C | H | N | E | G | ?D | U |
| Black River | I | H | N | E | S | C | U |
| Spaanschemat River | I | H | LW | E | G | C | U |

inundated. The seasonality of flow is recorded (winter only or none). Where there was water movement this is subjectively described as high or low, where flow was high if it obviously moved shoots growing in the water and low if the shoots remained still but water moment was observed. The nutrient status of vlei waters is described as eutrophic if total phosphorus concentration was between 25 and 30ugP $l^{-1}$ and nitrate-nitrogen was between 0.5 and 1.0mgN $l^{-1}$, or mesotrophic if they were lower than this (Wetzel, 1975). Bank slope is described as steep if it exceeded 60° (basin-shaped), or gentle if it was less than 60° (i.e. saucer-shaped). Changes in soil or water salinity are described as increasing or decreasing where there is evidence to support this. Finally, changes in littoral plant cover are indicated where the banks have either been cleared artificially or drawdown has resulted in plant death.

In all vleis where *Typha* appeared to be encroaching, water supply had increased, and in most cases (10 out of 11) this had resulted in decreased seasonal water level fluctuations (Table 3.6). While water supply had also increased in many vleis without an encroachment problem, in these water level fluctuations were usually large. Exceptions were Princessvlei, Little Princessvlei, the Strandfontein maturation ponds and Big Lotus River, all of which had steeply-banked littoral zones which prevented *Typha* encroachment. High concentrations of nutrients were common to vleis where encroachment has been recorded and where stand size did not appear to be changing. Encroachment was generally associated with vleis where there was little or no flow. A reduction in salinity levels has only been measured in the Noordehoek salt pans where there has been *Typha* invasion and encroachment.

From this survey the following factors were identified as apparently being related to the spread of *Typha* in the south-western Cape:

1. Increase in unseasonal water supply which results in relatively high soil moisture levels during summer. This is supported by the fact that *Typha* invades littoral zones which remain damp for most of the summer (e.g. Fiala & Kvet, 1971; Grace & Harrison, 1986).
2. Reduced fluctuations in water level, often associated with a reduction in maximum water depth. This prevents rushes from being drowned during winter and may be the result of anthropogenic activities such as weir or dam building, or may be a natural phenomenon such as siltation (Weisser, 1978; Kalk *et al.*, 1979).
3. Creation of areas suitable for germination and seedling establishment by drawdown, clearing, or by reduction in soil or water salinity. Drawdown is often associated with the invasion of wetlands by primary colonisers such as *Typha*, which require shallow water to become established, but which can tolerate deeper water when mature (Gaudet, 1977; Bonnewell *et al.*, 1983).

As water supply and depth were the most important variables governing *Typha* distribution, it is not surprising that these factors influence the ultimate size of rushbeds. In the south-western Cape, summer growth around lake margins is usually limited by water supply (Chapter 4). For this reason, wetlands which are flooded in winter but which are dry in summer (like the Glencairn Wetland), are not subject to encroachment. If, however, the water supply is stabilised by reducing summer drawdown, the water supply to the marginal stands is maintained, enhancing plant growth and bed encroachment. Alternatively, if water depth is reduced, areas suitable for rush growth are created. This could be the result of siltation that raises the wetland floor, or of artificial drawdown over a gently sloping basin. The former has

been recorded around the mouth of Rietvlei, Princessvlei, Little Princessvlei and Langvlei, while an example of the latter is provided by Rondevlei.

Rondevlei is a good example of rushbed encroachment in response to alteration of the natural hydrological regime. In the 1930s the wetland had no marginal rushbeds. *Typha* was excluded from the vegetation assemblage by two factors: periodic salinity intrusion via the Zeekoevlei Canal, and large seasonal fluctuations in marginal soil moisture (Hutchinson *et al.*, 1932; Howard-Williams, 1980). The first *Typha* stand appeared soon after a rubble weir was built to stabilise the water level both of Rondevlei and of Zeekoevlei (Middlemiss, 1974) (Fig. 3.12a). This weir was subsequently replaced by a more permanent structure which maintained the water level in Rondevlei at an even lower and more constant depth resulting in an extended marshy area around the vlei (Middlemiss, 1974). This was quickly colonised by new *Typha* stands. At a later date, the maximum water level was further reduced in order to create sand banks for wading birds. Due to the saucer-shaped basin of the vlei, these changes exposed a proportionately greater area of shoreline. Contrary to expectations, the sandbanks were quickly colonised by the wetland grass, *Paspalum vaginatum* and by new *Typha* stands (Fig. 3.12b).. During this period (1953 - 1975), Rondevlei was still a seasonal water body which completely dried up periodically. Recent hardening of the catchment has, however, increased the volume of runoff by as much as 30% (Thornton, cited in Darroch, 1988), and so have reduced the degree of drawdown. This reduction in seasonal water-level fluctuations has promoted marginal spread of the rushbeds. By 1983, bulrush beds had almost encircled the vlei (Fig. 3.12c), and by 1987 their encroachment into the vlei was becoming obvious (Fig. 3.12d).

There were exceptions to these general principles governing encroachment. For example, management

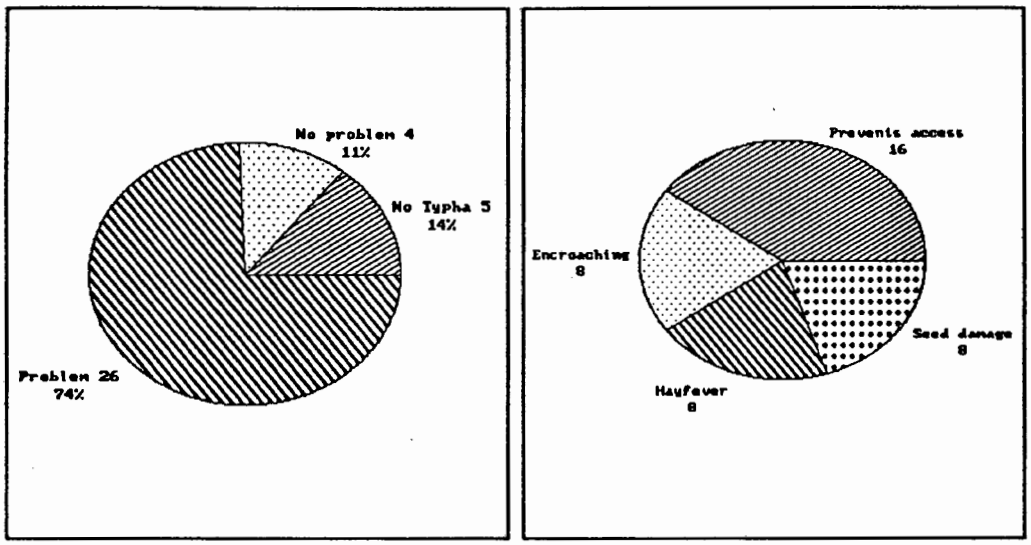
records indicated that some of the wetlands which did not appear suffer encroachment have a history of reduced seasonal drawdown (Little Princessvlei and Princessvlei). Theoretically, they should have been vulnerable to encroachment. Instead, large rushbeds at their mouths and at their outflows, as well as in small, isolated beds around their perimeters (Fig. 3.11) had formed, but were not spreading. Examination of marginal stands revealed that they were confined to areas where the dredged, steeply sloping banks had collapsed, forming shallow, sloping areas. The exclusion of *Typha* on steeply sloped, or on shelving banks suggests that encroachment in these vleis has been resisted by dredging of the vlei margins. Encroachment from existing *Typha* stands was inhibited by deep-water channels. This finding is supported by reports that basin deepening is used to control reed swamp invasion elsewhere (Haslam, 1973).

Less important as a means of resisting invasion are shaded marginal areas where germination is light-limited. Although the present study collected no evidence to support this hypothesis, research elsewhere has shown that *Typha* germination and seedling establishment requires very specific light conditions (Bonnewell *et al.*, 1983; Finlayson *et al.*, 1983; Grace, 1984). These conditions were obviously met when wetland margins were cleared to gain access to the Rondevlei rushbeds during this study, because the sandbanks were quickly covered by a mat of *Typha* seedlings.

**ZEEKOEVLEI RESIDENTS SURVEY**

Thirty-five questionnaires were returned in the month following distribution. The majority of respondents (26) regarded *Typha* as a problem plant (Fig. 3.14), and all of those with *Typha* growing on their property noted that they had tried to remove it on a regular basis. The people who did not consider the rushbeds a problem argued that the advantages of the rushbeds,

primarily the creation of bird habitat and provision of privacy, outweighed their disadvantages.




(a) (b)

**Figure 3.14:** Pie charts illustrating the response of Zeekoevlei residents to the survey conducted to establish their views on the plant. The responses are (a) Is *Typha* a problem on your property? and (b) What problems does *Typha* cause (from the 26 respondents who reported a *Typha* problem)?

Of those respondents who did consider *Typha* a problem, most complained that the beds were so dense that they prevented access to the water. A smaller proportion found that *Typha* replaced other plants or was invading their lawns, while others complained of hayfever during the flowering period. The latter group could not be sure that *Typha* was the cause of their respiratory problems, but did complain that they were worst in December and January, the period when *Typha* pollen is shed (Chapter 4). The possibility that *Typha* pollen could be an allergenic substance was confirmed by medical experts (van Warmelo, 1989), although there is no epidemiological evidence linking the plant to incidents of asthma or bronchial disease (Thornton & Boddington, 1989). A small proportion of respondents complained that the seeds became embedded in soft furnishings, but none felt that they caused permanent damage. Nevertheless, there have been cases when the Cape Town City Council has had to make good damage done to curtaining and carpets in homes adjacent to *Typha* stands (Thornton & Boddington,

1989).

*Typha* is considered a weed by the majority of people living close to rushbeds. Most residents included in the survey were obliged to clear their water frontage at least annually to maintain access to the water, and all asked for advice on how best they could achieve long-term control. Nonetheless, none asked that *Typha* be completely eradicated.

## GENERAL DISCUSSION

The data presented on the distribution and spread of *Typha* in the south-western Cape show that the perceived spread within wetlands is real and that the species is considered a problem both by residents directly affected by the plant and by wetland managers.

Before the rushbeds are condemned, however, their role in the wider environmental context should be evaluated with a view to formulating management programmes. The advantages and disadvantages of rushbeds should be weighed against the alternatives of either having no emergent macrophyte beds or having another species replace them. A literature review was conducted in this regard, the results of which (Tables 3.7 and 3.8) indicate that a wetland with *Typha* beds has many advantages over one without them. Furthermore, *Typha* stands appear to cause no more problems than those of other emergent macrophytes. In all cases, problems are exacerbated when the beds increase in size and density (Sculthorpe, 1967). In addition to the changes listed (Table 3.8), spreading emergent macrophyte stands will:

1. Choke lake margins, preventing access to the water for recreation and management purposes (Axelsen & Julian, 1988; Thornton & Boddington, 1989; Langley, 1989);
2. Reduce the area of water available for recreation and as wading bird habitat

**Table 3.7** A summary of the role played by, and advantages of having, emergent plant stands in wetlands. * indicates roles which *Typha* plays but *Phragmites* does not.

| USE OR ADVANTAGE | REFERENCE |
|---|---|
| **ENVIRONMENTAL BENEFITS:** | |
| Habitat for birds | Finlayson *et al.*, 1983 |
| | Axelsen & Julian, 1988 |
| | Linde *et al.*, 1976 |
| | Langley, 1987 |
| Bank stabilisation | Axelsen & Julian, 1988 |
| | Brookes, 1985 |
| Substratum for invertebrates | Cantrell, 1979 |
| **WASTEWATER PURIFICATION** | |
| Litter trapping | Thornton & Boddington, 1989 |
| | Langley, 1989 |
| Nutrient removal | Finlayson & Chick, 1983 |
| | Reddy, 1983 |
| | Reddy *et al.*, 1982 |
| | van Oertzen & Finlayson, 1984 |
| | Gersberg *et al.*, 1986 |
| Heavy metal removal* | Blake *et al.*, 1984 |
| | Babcock *et al.*, 1983 |
| | Taylor & Crowder, 1983, 1986 |
| Rhizosphere oxidation | Dunbabin *et al.*, 1988 |
| Reduction in evaporation from water surface | Idso & Anderson, 1988 |
| | Smid, 1975 |
| **COMMERCIAL CROP** | |
| Material for Craft Work | Morton, 1976 |
| weaving | van der Toorn *et al.*, 1990 |
| | Marsh, 1955 |
| | Handoo *et al.*, 1988 |
| paper making | Marsh, 1955 |
| | Schery, 1954 |
| Ornamental plant* | Morton, 1975 |
| Cossack asparagus* | Sculthorpe, 1967 |
| | Turner, 1981 |
| Typhasterol* | Schneider *et al.*, 1983 |
| Fibre | Finlayson *et al.*, 1983 |
| Bioenergy | Pratt & Andrews, 1980 |
| Thatching | Sharma, 1978 |
| | van der Toorn *et al.*, 1990 |
| | Bruton, 1979 |
| **FOOD:*** | |
| Subsistence crop | Fox & Young, 1982 |
| | Morton, 1975 |
| | Babcock *et al.*, 1983 |
| | Schery, 1954 |
| | Turner, 1981 |
| Stock feed | Marsh, 1955 |
| **SOIL IMPROVEMENT:** | |
| Green manure | Morton, 1975 |
| Reducing soil salinity | Grace & Harrison, 1986 |
| | Marsh, 1955 |

**Table 3. 8:** Summary of the ways in which *Typha* beds alter wetlands and the implications for management. * indicates roles *Typha* plays that another emergent would not.

| ALTERATIONS OR MANAGEMENT PROBLEMS | REFERENCE |
|---|---|
| **ALTERATIONS** | |
| Increased siltation | Grace & Harrison, 1986<br>Weisser, 1978<br>Grindley & Dudley, 1988 |
| Increased rate of hydrosere succession | Gorham *et al.*, 1979<br>Sculthorpe, 1967<br>Gunnison *et al.*, 1985 |
| Increased nutrient loading by: | |
| litter fall | Dykyjova, 1978<br>Mason & Bryant, 1975<br>Davis, 1991<br>Howard-Williams & Howard-Williams, 1978<br>Howard-Williams, 1979 |
| guano production by nesting birds | McColl & Burger, 1976<br>Hayes & Caslick, 1984 |
| Increased water loss (evapotranspiration) | Morton, 1975<br>Grace & Harrison, 1986 |
| Restricted species diversity | Beule, 1979<br>Fiala & Kvet, 1971 |
| **MANAGEMENT PROBLEMS:** | |
| Breeding ground for disease vectors: | |
| midges | Cantrell, 1979 |
| mosquitoes | Axelsen & Julian, 1988 |
| Impeded drainage and water circulation | Axelsen & Julian, 1988<br>Grace & Harrison, 1986<br>Howard-Williams, 1983<br>Finlayson *et al.*, 1983<br>Thornton & Boddington, 1989<br>Sale & Orr, 1986 |
| Increased flooding | Finlayson *et al.*, 1983 |
| Presence of seeds and pollen: * | |
| irritants (skin, eye/ respiratory) | Thornton & Boddington, 1989<br>Finlayson *et al.*, 1983 |
| damage to soft furnishings | Thornton & Boddington, 1989<br>Finlayson *et al.*, 1983<br>Grace & Harrison, 1986 |
| Difficult to control | Nelson & Dietz 1960,<br>Beule, 1979<br>Weller, 1975 |

(Kantrud, 1986; Thornton & Boddington, 1989; Langley, 1989);

3. Reduce habitat diversity (Weller & Frederickson, 1974; Beule, 1979; Langley, 1989), which makes the vleis less suitable for water birds (Kantrud, 1986; Mallik & Wein, 1986);
4. Reduce the water storage capacity of reservoirs (Agronomy Department, 1973).

The problem is not the plant species, but it's life-form - dense, monospecific stands. Experience has shown that this life-form is often associated with wetlands which are vulnerable to the development of monotypes because they have low-gradient shorelines, uniform sediment types and restricted water-level fluctuations (Denny, 1985; Kantrud, 1986; Krusi & Wein, 1988). Emergent macrophyte beds are typical of the late successional stages of wetlands, but their development and persistence occur only in the absence of natural perturbations in the abiotic environment. By returning the community to a less stable state, disturbance maintains diversity (White, 1979; Greening & Gerritsen, 1987).

For example, in the Prairie potholes region of Canada, wetland vegetation follows a five- to thirty-year cycle in response to changes in the water regime (van der Valk, 1985). Open-water marshes, colonised by submerged and free-floating macrophytes, become dry marshes in response to drawdown during drought periods. The damp margins are colonised by reeds and rushes, which spread as the marsh basin is refilled by normal rainfall, which eventually causes the decline of emergent populations. This process is enhanced by the damage caused to rushbeds by muskrats, whose numbers increase during the regenerating marsh stage. The combination of high water levels and herbivory kills the emergents and the wetland returns to the open-water marsh stage.

Both shorter and longer cycles have been reported. For example, Gaudet (1977) describes three vegetation zones, open-water, sedge-dominated and composite-dominated, which develop during summer drawdown of Lake Naivasha, Kenya. As the basin is reflooded, the central sedge zone expands in both directions so that it dominates the littoral zone during winter. At the other extreme, Lake Rukwa in Tanzania dries up only every three to four centuries, returning the lake to the open water stage (Gunn, 1973, cited in Howard-Williams, 1979).

The dynamic nature of water regimes is the driving force behind change in macrophyte community structure (Howard-Williams, 1975; van der Valk & Davies, 1980; Farney & Bookhout, 1982; Keddy & Reznicek, 1982; Kantrud, 1986; Klimas, 1988; Krusi & Wein, 1988). Seasonal and long-term water level changes are natural components of the wetland environment. The vegetation of such habitats is specifically adapted to these changes and merely responds to them through oscillating shifts in species dominance (Gopal, 1986; Greening & Gerritsen, 1987). As the frequency, magnitude or predictability of water-level fluctuations increases, the number of species adapted to the site decreases (Greening & Gerritsen, 1987; Klimas, 1988). The removal of disturbance altogether stabilises the climax state (Murkin & Ward, 1980; Weisser & Howard-Williams, 1982), enhancing hydrosere succession (Lieffers, 1983; Krusi & Wein, 1988).

It is clear that the problem faced is not one of *Typha* encroachment, but rather is related to the management of the wetlands themselves. Artificial dampening of wetland flood regimes has created an environment which promotes emergent encroachment by the most competitive species. The only permanent solution to the problem of encroachment is to promote competitive replacement by reintroducing disturbance, possible as a dynamic hydrological regime.

## CONCLUSIONS

1. *Typha capensis* is found throughout the study area. Its distribution appears to be restricted to areas which remain damp throughout summer and which have gently-sloping banks. It is not found in areas where there is strong flow, steep banks, high salinity or water depths exceeding 1.2 m.

2. Rushbeds are encroaching on many of the vleis visited. Encroachment is associated with the reduction in seasonal water-level fluctuations, especially in areas with saucer-shaped basins and gently-shelving shorelines.

3. The most accurate estimate of short-term spread indicates that *Typha* encroaches at a rate of approximately 1.5 m month$^{-1}$.

4. The management problems caused by rushbeds are considerable, but the beds play an important role in many of our local wetlands. The problems are related to dense monospecific stands of emergent species, not specifically *Typha* stands. Their replacement by another species is thus unlikely to eliminate, or even to reduce, wetland management problems.

### REFERENCES

AGRONOMY DIVISION, 1973. Cumbungi - a menace to water storage. *Tas. J. Agric.*, 13: 86-90.

ALLEN, S.E., GRIMSHAW, H.M. & ROWLAND, A.P. 1986. Chemical analysis. In: *Methods in Plant Ecology*. Moore, P.D. & Chapman, S.B. (eds). Blackwell Scientific Publications, Oxford.

AXELSON, S. & JULIAN, C. 1988. Weed control in small dams. Part 1. Introduction: Control of algae and of cumbungi. *Queensland Agric. J.*, July-Aug.: 241-246.

AZORIN, E.J., 1988. *Distribution of plant communities in the wetlands of Zandvlei*. Unpublished report for the Town Planning Branch, Cape Town City Council Planners Department, Cape Town.

BABCOCK, M.F., EVANS, D.W. & ALBERTS, J.J. 1983. Comparative uptake and translocation of trace elements from coal ash by *Typha latifolia*. *Sci. Tot. Environ.*, 28: 203-214.

BEARE, P.A. & JEDLER, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh - the role of salinity intrusion. *Estuaries*, 10: 165-170.

BEULE, J.D. 1979. *Control and management of cattails in south-eastern Wisconsin wetlands*. Tech. Bull. No. 112. Dept. Nat. Res., Madison, Wisconsin.

BLAKE, G., GRAGNAIRE-MICHARD, J. & KIRASSIAN, B. 1984. Accumulation of zinc (Zn65) by a macrophyte, *Typha latifolia*. *Rev. Fr. Sci. Eau/Fr. J. Water Sci.*, 3: 750-786.

BONNEWELL, V., KOUKKARI, W.L. & PRATT, D.C. 1983. Light, oxygen and temperature requirements for *Typha latifolia* seed germination. *Can. J. Bot.*, 61: 1330-1336.

BOUCHER, C. 1988. Wetland vegetation in the Fynbos Biome. In: *Hydrology and hydrobiology in the Fynbos Biome*. King, J.M. (ed.). Foundation for Research and Development Occasional Report No. 26, CSIR, Pretoria.

BRAND, J.C. 1983. *Overcoming environmental constraints upon the development of Khayelitsha*. Cape Town City Council Report, Cape Town.

BROOKES, A. 1985. River cannelisation: Traditional engineering methods, physical effects and alternative practices. *Prog. Physical Geog.*, 9: 44-73.

BRUMMER, T.B. 1981. *A development plan for the Zeekoevlei Complex*. MSc Thesis, Department of Town and Regional Planning, University of Stellenbosch, Stellenbosch.

BRUTON, M.N. 1979. The utilisation and conservation of L. Sibaya. In: *Lake Sibaya*. Allanson, B.R. (ed.). Dr W. Junk Publishers, The Hague.

CANTRELL, M.A. 1979. Invertebrate communities in the Lake Chilwa swamp in years of high level. In: *Lake Chilwa: Studies of change in a tropical ecosystem*. Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds). Dr W. Junk Publishers, The Hague.

DARROCH, A. 1988. *Zandvlei catchment land use*. Zandvlei Working Group interim technical report, Town Planning Branch, City of Cape Town, Cape Town.

DAVIES, B.R. 1983. *Report on reed removal at Zeekoevlei and commentary on aerial photographs (1968 and 1980) showing the development of emergent and submerged vegetation in the vlei*. Unpublished report No. 6, Cape Town City Council, Cape Town.

DAVIS, S.M. 1991. Growth, decomposition and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat. Bot.*, 40: 203-224.

DAY, J.A. & KING, J.M. 1980. *The limnology of the Cape Flats*. Unpublished Report, Department of Zoology, University of Cape Town, Cape Town.

DAY, J.H., SIEGFRIED, R., LOUW, R.W. & JARMAN, A.J. 1979. *Fynbos ecology*. South African National Programmes Report No. 40, CSIR, Pretoria.

DENNY, P. 1985. Wetland vegetation and associated plant life-forms. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, Dordrecht.

DICK, R.I. 1983. *Settling characteristics of the mud and chemical characteristics of the interstitial water at Princessvlei*. Ref C.B.2/V1, Scientific Services Branch, Cape Town City Council, Cape Town.

DUNBABIN, J.S., POKORNY, J. & BOWMER, K.H. 1988. Rhizosphere oxygenation by Typha domingensis Pers. in miniature artificial wetland filters used for metal removal from wastewater. *Aquat. Bot.*, 29: 303-317.

DYKYJOVA, D. 1978. Nutrient uptake by littoral communities of helophytes. In: *Pond Littoral Ecosystems: Structure and functioning*. Dykyjova, D. & Kvet, J. (eds). Ecological Studies, 28. Springer-Verlag, Berlin.

FARNEY, R.A. & BOOKHOUT, T.A. 1982. Vegetation changes in a Lake Erie marsh (Winous Point, Ottawa Country, Ohio) during high water years. *Ohio J. Sci.*, 82: 103-107.

FIALA, K. & KVET, J. 1971. Dynamic balance between plant species in South Moravian reedswamps. In: *The Scientific Management of Animal and Plant Communities for Conservation*. Duffey, E. & Watt, A.S. (eds). Blackwell Scientific Publications, Oxford.

FINLAYSON, C.M. & CHICK, A.J. 1983. Testing the potential of aquatic plants to treat abattoir effluent. *Water Res.*, 17: 414-422.

FINLAYSON, C.M., ROBERTS, J., CHICK, A.J. & SALE, P.J.M. 1983. Biology of Australian weeds. II. *Typha domingensis* Pers. and *Typha orientalis* Presl. *J. Aust. Inst. Aquat. Weeds*, 49: 3-10.

FOX, F.W. & YOUNG, M.N. 1982. *Food from the Veld*. Delta Books, Johannesburg.

FURNESS, H.D. 1979. *Report on ecological conditions at Zandvlei during 1979*. Report to Scientific Services Branch, Cape Town City Council, City Engineers Department, Cape Town.

GARDINER, A.J.C. 1988. *A study on the water chemistry and plankton in blackwater lakelets of the Southwestern Cape*. PhD Thesis, Department of Zoology, University of Cape Town, Cape Town.

GAUDET, J.J. 1977. Natural drawdown on Lake Naivasha, Kenya and the formation of papyrus swamps. *Aquat. Bot.*, 3: 1-47.

GERSBERG, R.M., ELKINS, B.V., LYON, S.R. & GOLDMAN, C.R. 1986. Role of aquatic plants in wastewater treatment by artificial wetlands. *Water Res.*, 20: 363-368.

GODSHALK, G.L. & BARKO, J.W. 1985. Vegetative succession and decomposition in reservoirs. In: *Microbial Processes in Reservoirs*. Gunnison, D. (ed.). Dr W. Junk Publishers, Dordrecht.

GOPAL, B. 1986. Vegetation dynamics in temporary and shallow freshwater habitats. *Aquat. Bot.*, 23: 391-396.

GORHAM, E., VITOUSEK, P.M. & REINERS, W.A. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Ann. Rev. Ecol. Syst.*, 10: 53-84.

GRACE, J.B. 1984. Effects of tubificid worms on the germination and establishment of *Typha*. *Ecology*, 65: 1689-1693.

GRACE, J.B. & HARRISON, J.S. 1986. The biology of Canadian weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha glauca* Godr. *Can. J. Plant Sci.*, 66: 361-379.

GREENING, H.S. & GERRITSEN, J. 1987. Changes in macrophyte community structure following drought in the Okefenokee Swamp, Georgia, U.S.A. *Aquat. Bot.*, 28: 113-128.

GRINDLEY, J.R. & DUDLEY, S. 1988. *Estuaries of the Cape. Part II. Synopses of available information on individual systems. Report No. 28: Rietvlei (CW24) and Diep Estuary (CW25).* CSIR Research Report 427, Stellenbosch.

GRINDLEY, S.A. 1984. *A study of land-use patterns in the Hout Bay catchment with reference to the degradation of the river canal.* MSc Thesis, School of Environmental Studies, University of Cape Town, Cape Town.

GRINDLEY, S.A. 1988. *Estuaries of the Cape. Part II. Synopses of available information on individual systems.* Report No. 29: Hout Bay (CW27). CSIR Research Report 428, Stellenbosch.

GUNNISON, D., ENGLER, R.M. & PATRICK, W.H.Jr. 1985. Chemistry and microbiology of newly flooded soils: Relationship to reservoir water-quality. In: *Microbial Processes in Reservoirs.* Gunnison, D. (ed.). Dr W. Junk Publishers, Boston.

HAM, S.F., WRIGHT, J.F. & BERRY, A.D. 1982. The effect of cutting on the growth and recession of the freshwater macrophyte *Ranunculus penicillatus* (Dumort.) Bab. var. *calcareus* (R.W. Butcher) C.D.K. Cook. *J. Environ. Mngmt.*, 15: 263-271.

HANDOO, J.K., SARAF, N. & KAUL, V. 1988. Energy content and ecological efficiency of macrophytes in Dal Lake, Kashmir. *Arch. Hydrobiol.*, 111: 351-367.

HARDING, W.R. 1991. *Ecology of Urban-Impacted Coastal Vleis on the Cape Flats near Cape Town, with special reference to Phytoplankton Periodicity.* MSc Thesis, Department of Zoology, University of Cape Town, Cape Town, South Africa.

HASLAM, S.M. 1973. The management of British wetlands. II. Conservation. *J. Environ. Mngmt.*, 1: 345-361.

HAYES, J.P. & CASLICK, J.W. 1984. Nutrient deposition in cattail stands by communally roosting blackbirds and starlings. *Am. Midl. Nat.*, 112: 320-331.

HEINECKEN, T.J.E. 1982. *Estuaries of the Cape. 2. Synopses of available information on individual systems. Report No. 13: Silvermine (CSW 3).* CSIR Research Report No. 412, Stellenbosch.

HEINECKEN, T.J.E. 1985. *Estuaries of the Cape. 2. Synopses of available information on individual systems. Report No. 27. Wildevoelvlei/Noordehoek (CW28).* CSIR Research Report No. 426, Stellenbosch.

HOWARD-WILLIAMS, C. 1975. Vegetation changes in a shallow African lake. Response of the vegetation to a recent dry period. *Hydrobiologia*, 47: 381-389.

HOWARD-WILLIAMS, C. 1976. *Proposals for an ecological investigation of surface waters in the Cape Peninsula.* Report to National Programme for Environmental Sciences and the Water Research Commission. Rhodes University, Grahamstown.

HOWARD-WILLIAMS, C. 1979. The distribution of aquatic macrophytes in Lake Chilwa: Annual and long-term fluctuations. In: *Lake Chilwa: Studies of change in a tropical ecosystem.* Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds). Dr W. Junk Publishers, The Hague.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophyte communities of the Wilderness Lakes: Community structure and associated environmental conditions. *J. Limnol. Soc. sth. Afr.*, 6: 85-92.

HOWARD-WILLIAMS, C. 1983. Wetlands and watershed management; the role of aquatic vegetation. *J. Limnol. Soc. sth. Afr.*, 9: 54-62.

HOWARD-WILLIAMS, C. & HOWARD-WILLIAMS, W. 1978. Nutrient leaching from the swamp vegetation of Lake Chilwa, a shallow African lake. *Aquat. Bot.*, 4: 257-267.

HUTCHINSON, G.E., PICKFORD, G.E.& SCHUURMAN, J.F.M. 1932. A contribution to the hydrology of pans and other inland waters of South Africa. *Arch. Hydrobiol.*, XXIV: 1-154.

IDSO, S.B. & ANDERSON, M.G. 1988. A comparison of two recent studies of transpiration water loss from emergent aquatic macrophytes. *Aquat. Bot.*, 31: 191-195.

JOHNSON, W.B., SASSER, C.D. & GOSSELINK, J.G. 1985. Succession of vegetation in an evolving river delta, Atchafalaya Bay, Louisiana. *J. Ecol.*, 73: 973-986.

KALK, M.J., MCLACHLAN, A.J. & HOWARD-WILLIAMS, C. (eds). 1979. *Lake Chilwa: Studies of change in a tropical ecosystem.* Monogr. Biol., 35: Dr W. Junk Publishers, The Hague.

KANTRUD, H.A. 1986. *Effects of vegetation manipulation on breeding waterfowl in Prairie wetlands - a literature review.* Fish and Wildlife Technical Report 3, Washington D.C.

KEDDY, P.A. & REZNICEK, A.M. 1982. The role of seed-banks in the persistence of Ontario's coastal plain flora. *Am. J. Bot.*, 69: 13-22.

KENKEL, N.C. 1987. Trends and interrelationships in boreal wetland vegetation. *Can. J. Bot.*, 65: 12-22.

KLIMAS, C.V. 1988. River regulation effects on floodplain hydrology and ecology. In: The *Ecology and Management of Wetlands. 1. Ecology* of wetlands. Hook, D.D., KcKee, W.H., Smith, H.K., Gregory, J., Burrell, V.G., DeVoe, M.R., Sojka, R.E., Gilbert, S., Banks, R., Stolzy, L.H., Brooks, C., Matthews, T.D. & Shear, T.H. (eds). Croom Helm, London.

KRUSI, B.O. & WEIN, R.W. 1988. Experimental studies as the resiliency of floating *Typha* mats in a freshwater marsh. *J. Ecol.* , 76: 60-72.

KSENOFONTOVA, T. 1989. General changes in the Matsulu bay reedbeds in this century and their present quality (Estonian SSR). *Aquat. Bot.*, 35: 111-120.

LANGLEY, C.H. 1987. *Notes on Typha latifolia: A threat to our wetlands.* Unpublished report. Rondevlei Bird Sanctuary, Cape Town.

LANGLEY, C.H. 1989. Problems caused by *Typha*. In: *Typha: Its status, problems, economic benefits and control.* van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

LIEFFERS, V.J. 1983. Growth of *Typha latifolia* in Boreal forest habitats, as measured by double sampling. *Aquat. Bot.*, 15: 335-348.

LINDE, A. F., JANISCH, T. & SMITH, D. 1976. *Cattail: The significance of its growth, phenology and carbohydrate storage to its control and management.* Tech. Bull. 94, Department of Natural Resources, Madison, Wisconsin.

MALLIK, A.U. & WEIN, R.W. 1986. Response of a Typha marsh to draining, flooding and seasonal burning. *Can. J. Bot.*, **64**: 2136-2143.

MANNING, J.H. & SAUNDERS, D.R. 1975. Effect of water level fluctuation on vegetation in Black Lake, Louisiana. *Hyacinth Control J.*, **13**: 17-21.

MARSH, L.C. 1955. The cattail story. *Garden J.*, **5**: 114-129.

MASON, C.F. & BRYANT, R.J. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, **63**: 71-95.

MCCOLL, J.G. & BURGER, J. 1976. Chemical inputs by a colony of Frankins Gulls nesting in cattails. *Am. Midl. Nat.*, **96**: 270-280.

MIDDLEMISS, E. 1974. *The Rondevlei Bird Sanctuary. A record of the environment, 1952-1974*. Divisional Council of the Cape, Cape Town.

MOORE, P.D. & CHAPMAN, S.B. 1986. *Methods in Plant Ecology*. (2nd ed.). Blackwell Scientific Publications, Oxford.

MORANT, P.D. & GRINDLEY, J.R. 1982. *Estuaries of the Cape. 2. Synopses of available information on individual systems. Report No. 14: Sand (CSW4)*. CSIR Research Report 413, Stellenbosch.

MORRISON, I.R. 1982. *Survey of water quality in the Black River Catchment, 1968-1980*. City Engineers Report, Scientific Services Branch, Cape Town City Council, CB 2/R4, Cape Town.

MORTON, J.F. 1975. Cattails (*Typha* spp.) - Weed problem potential crop. *Econ. Bot.*, **29**: 7-29.

MORTON, J.F. 1976. Craft industries from coastal wetland vegetation. In: *Estuarine Processes. 1. Uses, Stresses and Adaptation to the Estuary*. Wiley, M. (ed.). Academic Press, New York.

MOSTERT, S.A. 1983. Procedure used in South Africa for the automatic photometric determination of micronutrients in seawater. *S. Afr. J. Mar. Sci.*, **1**: 189-198.

MUIR, D. 1974. *The ecology of Sandvlei*. Honours Project, Department of Zoology, University of Cape Town, Cape Town.

MURKIN, H.R. & WARD, P. 1980. Early spring cutting to control cattail in a northern marsh. *Wildl. Soc. Bull.*, **8**: 254-256.

NAPPER, D.M. 1971. Typhaceae. *Flora Trop. East Afr.*

NELSON, N.F. & DIETZ, R.H. 1960. *Cattail control methods in Utah*. Utah State Department of Fish and Game Publication No. 66-2.

PARKER, D. 1982. The western Cape lowland fynbos. What is there left to conserve? *Veld and Flora*, **68**: 98-101.

PRATT, D.C. & ANDREWS, N.J. 1980. Cattails (*Typha* spp.) as an energy source. In: *Energy from Biomass and Wastes*. White, J.W., McGrew, W. & Suttor, M.R. (eds). Florida.

QUICK, A.J.R. 1987. *The biology, economic importance and management of the bulrush Typha latifolia (L.) with emphasis on the use of wetlands for improving water quality*. Report for the Town Planners Branch, Cape Town City Planners Department, Cape Town.

REDDY, K.R. 1983. Nitrogen and phosphorus interchange between sediments and overlying water of a wastewater retention pond. *Hydrobiologia*, 98: 237-243.

REDDY, K.R., CAMPBELL, K.L., GRAETZ, D.A. & PORTIER, K.M. 1982. Use of biological filters for treating agricultural drainage effluents. *J. Environ. Qual.*, 11: 591-595.

ROBERTS, J. 1987. *The autocology of Typha spp. in South-Eastern Australia*. PhD Thesis, Department of Botany, University of Adelaide, Australia.

ROMAN, T., ROMAN, L., RADUCA, C. & MOLNAR, A. 1985. Interaction between some environmental factors in the Danube Delta on the delimitation of the vital space occupied by the reed, mace reed and the sedge, cenoses. *Arch. Hydrobiol.*, **68**: 149-162.

RUDNICK, G. 1986. *Report on the ecological conditions at Zeekoevlei during 1984*. City Engineers Department, Scientific Services Branch, Cape Town City Council, Cape Town.

SALE, P.J. & ORR, P.T. 1986. Gas exchange of *Typha orientalis* Presl. communities in artificial ponds. *Aquat. Bot.*, **23**: 309-320.

SCHERY, R.W. 1954. *Plants for Man*. George Allen and Unwin Ltd., London.

SCHNEIDER, J.A., YOSHIHARA, K & NAKANISHI, K. 1983. Typhasterol (2-deoxycasterone): A new plant growth regulator from cattail protein. *Tetragedron Letters*, 24: 3859-3860.

SCULTHORPE, C.D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold Publishers, London.

SEMMELINK, M.M. 1990. *An introduction to the phosphorus dynamics in Rondevlei*. MSc Thesis, Department of Zoology, University of Cape Town, Cape Town.

SHARMA, K.P. 1978. Effect of cutting on the growth and flowering behaviour of *Typha elephantina* Roxb. *Current Sci.*, 47: 275-276.

SHAY, J.M. & SHAY, C.T. 1986. Prairie marshes in western Canada, with special reference to the ecology of five emergent macrophytes. *Can J. Bot.*, 64: 443-454.

SHELTON, P. 1975. *The ecology of Sandvlei*. Honours Project, Department of Zoology, University of Cape Town, Cape Town.

SILBERBAUER, M.J. & KING, J.M. 1991. Geographical trends in the water chemistry of wetlands in the south-western Cape Province, South Africa. *Sth. Afr. J. aquat. Sci.*, 17: 82-88.

SMID, P. 1975. Evaporation from a reedswamp. *J. Ecol.*, 299-310.

STEPHENS, E.L. 1929. Freshwater aquatic vegetation of the south-western districts. In: *The Botanical Features of the South-Western Cape Province*. Adamson, R.S. & Salter, T.M. (eds). Speciality Press, Cape Town.

TAYLOR, H.C. 1978. *Capensis*. In: *Biogeography and Ecology of Southern Africa*. Werger, M.J.A. & Bruggen, A.C. (eds). Monogr. Biol. 31. Dr W. Junk Publishers, The Hague.

TAYLOR, G.J. & CROWDER, A.A. 1983. Uptake and accumulation of copper, nickel and iron by *Typha latifolia* L. grown in a solution culture. *Can. J. Bot.*, 61: 1825-1830.

TAYLOR, G.J. & CROWDER, A.A. 1986. Uptake and accumulation of copper, nickel and iron by *Typha latifolia*. *Am. J. Bot.*, 70: 56-71.

THOMPSON, D.J. & SHAY, J.M. 1985. The effects of fire on *Phragmites australis* in the Delta marsh, Manitoba. *Can. J. Bot.*, 63: 1864-1869.

THORNTON, J.A. & BODDINGTON, G. 1989. Problems associated with the bulrush, *Typha latifolia*, in Cape Town. In: *Typha: Its status, problems, economic benefits and control*. van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

TOIVONEN, H. & BACK, S. 1989. Changes in aquatic vegetation of a small eutrophicated and lowered lake (Southern Finland). *Ann. Bot. Fennici.*, 26: 27-38.

TOIVONEN, H. & NYBOM, C. 1989. Aquatic vegetation and its recent succession in the waterfowl wetland Koijarvi, S. Finland. *Ann. Bot. Fennici.*, 26: 1-14.

TOWN PLANNING BRANCH, 1988. *Zandvlei*. Working Group Interim Technical Report. Cape Town City Council, Cape Town.

TURNER, N.J. 1981. A gift for the taking: The untapped potential of some food plants of North American native peoples. *Can. J. Bot.*, 59: 2331-2357.

VAN DER TOORN, J., VERHOEVEN, J.T. & SIMPSON, R.L. 1990. Freshwater marshes. In: *Wetlands and Shallow Continental Water Bodies*. Patten, B.C., Jorgenson, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

VAN DER VALK, A.G. 1985. Vegetation dynamics of prairie glacial marshes. In: *The Population Structure of Vegetation*. White, J. (ed.). Dr W. Junk Publishers, The Hague.

VAN DER VALK, A.G. & DAVIS, C.B. 1980. The impact of natural drawdown on the growth of four emergent species in a prairie glacial marsh. *Aquat. Bot.*, 9: 301-322.

VAN OERTZEN, I. & FINLAYSON, C.M. 1984. Wastewater treatment with aquatic plants: Ecotypic differentiation of *Typha domingensis* seedlings. *Environ. Poll.*, 35: 259-269.

VAN WARMELO, W. (ed.). 1989. *Typha: Its status, problems, economic benefits and control*. Botanical Society of South Africa, Cape Town.

WEISSER, P.J. 1978. A conceptual model of a siltation system in shallow lakes with littoral vegetation. *J. Limnol. Soc. sth. Afr.*, 4: 145-149.

WEISSER, P.J. 1979. *Report on the vegetation of the Wilderness Lakes and the macrophyte encroachment problem*. Report for the Botanical Research Institute, Pretoria.

WEISSER, P.J. & HOWARD-WILLIAMS, C. 1982. The vegetation of the Wilderness Lakes system and the macrophyte encroachment problem. *Bontebok*, 2: 19-40.

WEISSER, P.J. & STADLER, A. 1983. Suitability of aerial photographs for monitoring emergent and submerged macrophyte vegetation in the Wilderness Lakes, S. Africa. In: *Proceedings of the International Symposium on Aquatic Macrophytes*, Nijmegen.

WELLER, M.W. 1975. Studies of cattail in relation to management for marsh wildlife. *Iowa State J. Res.*, 49: 383-412.

WELLER, M.W. & FREDERICKSON, L.H. 1974. Avian ecology of a managed glacial march. *Living Bird*, 12: 269-291.

WESSELS, W.P.J. 1981. *The hydrology of the Cape Flats*. Report for the Cape Town City Council, Cape Town.

WETZEL, R.G. 1975. *Limnology*. Saunders Press, Philadelphia.

WHITE, P.S. 1979. Pattern, process and natural disturbance in vegetation. *Bot. Rev.*, 45: 229-299.

## APPENDIX 1

ARE BULRUSHES A PROBLEM IN THE ZEEKOEVLEI AREA?

NAME:.....

ADDRESS:.....

TELEPHONE NUMBER: ..... (H) ..... (W)

1. Do you own the property you live on? YES / NO

2. Are there any bulrushes (papkuil) plants growing on the property? YES / NO

3. If YES, has the number of shoots or the area covered by the plants increased over the past year? YES / NO
If so, by how much?
From approximately .....$m^2$ to .....$m^2$

4. In your opinion, do they cause any of the following problems:
-Block access to the water?
-Crowd out the plants growing near them?
-Skin irritation from seeds or pollen?
-Respiratory irritation from seeds or pollen?
-Damage to soft furnishings?
-Any other problems? .....

5. Have you ever tried to remove the plants? YES / NO

6. If so, how?
-regular cutting of leaves and stems?
How often: .....
-irregular cutting of leaves and shoots?
How often:.....

-regular digging up of rootstock? How often: .....

-irregular digging up of rootstock? How often:.....

-burning? How often:.....

-herbiciding? What herbicide do you use? .....

-other (please specify) .....

7. Are control measures successful? .....

.....

8. Do you have any other comments? .....

.....

.....

# CHAPTER 4

# THE EFFECT OF FLOOD REGIME ON THE PHENOLOGY, LIFE-HISTORY, GROWTH AND PRODUCTION OF *TYPHA CAPENSIS* IN THE SOUTH-WESTERN CAPE


## SUMMARY

Demographic techniques were adopted for study of phenological development, life-history traits and production by *Typha capensis* (bulrush) in Rondevlei, a freshwater marsh on the Cape Flats. Three growth phases were identified within the rushbeds. The senile phase was dominated by standing litter which restricted production by interfering with above and belowground growth. It was associated with the driest part of the littoral zone which was never flooded. The mature phase, associated with areas which were seasonally-flooded, was the most productive. Here, generative shoot density was high as a result of continuous recruitment of emergent shoots associated with low mortality rates. The juvenile phase was confined to areas which were always-flooded, or which were being colonised. It appears that winter flooding prevents the establishment of the mature phase in the always-flooded part of the littoral zone by increasing shoot mortality, thus preventing the establishment of emergent shoots produced during summer.


## INTRODUCTION

Information pertaining to the growth and development of emergent plant species contributes to the prediction of aquatic community behaviour (Brux *et al.*, 1987). Furthermore, an understanding of life-history and phenological development contributes to effective control by providing information about when the plant is most vulnerable to different control methods. Such information, together with estimates of productivity, is vital for the development of a practical management strategy for the control of bulrushes.

The productivity of *Typha* has been measured numerous times (e.g. Boyd, 1971; Kalk *et al.*, 1979; Roberts & Ganf, 1986; Hogg & Wein, 1987), but the majority of studies have taken place in North America and Canada, using *T. latifolia*, *T. angustifolia* and their hybrid, *T.* X *glauca* (e.g. McNaughton, 1966; Mason & Bryant, 1975; Pratt & Andrews, 1980). Notable exceptions are the studies by Roberts & Ganf (1986) on *T. orientalis* in Australia; of Howard-Williams (1980), who estimated the production of *T. capensis* in the Wilderness Lakes, South Africa, and of Gopal & Sharma (1984) on the Indian species, *T. elephantina*. In southern Africa the study of the productivity of emergent macrophytes has been neglected. Most wetland research requiring information regarding emergent production estimates have used results from work performed elsewhere, on other species. This, in effect, has forced the concept that African species are "ecological equivalents" of those from other parts of the world, an approach with many dangers which should be avoided, because gross environmental differences may have profound adaptive significance. There is, therefore, a strong case for studying all aspects of the biology of *T. capensis* under local conditions.

Until recently, most productivity studies used harvesting methods, reaping biomass as it was produced, in order to estimate production rates. There has, however, been a recent trend towards the use of demographic techniques designed to provide insights into life-history events that influence productivity (Bernard & MacDonald, 1974; Bernard, 1975; Bernard & Solsky, 1977; Bernard & Gorham, 1978; van der Toorn & Mook, 1982; Lieffers, 1983; Penko & Pratt, 1985/86). Frequent morphological measurements can be used to examine growth processes, turnover and resource allocation, and the analysis of population dynamics provides estimates of mortality, survivorship and longevity. These can all be used to improve the accuracy of production estimates (Tomlinson, 1974; Jefferies, 1984). In addition, such information is

vital where attempts are being made to explain year-to-year or site-to-site variation in production. For example, Dickerman (1982) was able to trace annual variations in production by examining the internal dynamics of cohort structure. Such information cannot be obtained by using simple harvest techniques, and accordingly, have been avoided in the study reported here.

Demographic techniques do, however, have their own problems. Firstly, they are time consuming. Fluxes can only be measured by marking and repeatedly measuring the same plant modules, for simple census techniques show no change if individuals replace each other (Harper, 1978). Secondly, fluxes have to be monitored for longer than one year if environmental influences on population dynamics are to be understood (Hultgren, 1988).

Additional problems relate to the application to clonal populations of plant population theories based on non-cloning species. The patterns and processes of growth in clonal species is still poorly understood, despite attention since 1979 (Noble *et al.*, 1979). The functional "individual" of a clonal species such as *T. capensis*, is the ramet, but these are subunits of the genetic individual, the genet. The latter is the equivalent to the functional individual in non-cloning species. As connections between ramets are usually underground, or have been lost as rhizome connections decompose, it is difficult to determine the extent of the genetic individual.

Harper (1978) suggested that genets can be considered as a number of modules which are repeatedly produced in the growth process. He further suggested that the demography of a population can be studied using any one of these modules that have properties associated with members of the population. For example, the smallest module of organised structure in higher plants is the leaf with its auxiliary bud. These

increase in number at an exponential rate, have juvenile, mature and senescent phases, birth rates, death rates and survivorship curves. They have been adequately used to describe the growth of plants under different environmental conditions (Williamson, 1976; Bazzaz & Harper, 1977).

In the past, both leaf and shoot demographic characteristics have been used in studies of *Typha* growth and life-history (Roberts, 1987; Dickerman, 1982). The study described here evaluated the use of the different plant modules to describe plant demography by comparing demographic trends revealed by the shoots of the population, with trends exhibited by the leaf structure of shoots. The demographic development of *Typha* was, however, modelled using data collected from ramet measurements.

The results of the survey examining the distribution and encroachment of *Typha* in the study area (Chapter 3) showed that deep water was one of four factors restricting rushbed distribution, and seasonal flooding appeared to play an important role in preventing their encroachment. For this reason the effect of maximum water depth and flooding regime on life-history characteristics and production was examined during the course of the study reported in this chapter. Specific objectives were to:

1. Describe the phenological development and life-history characteristics of *Typha* under local conditions;
2. Estimate production by *Typha* in a "typical" Cape Flats vlei, and
3. Evaluate the effect of local hydrological conditions on the phenology, life-history and production of *Typha*.

In addition, this work has provided baseline information regarding growth characteristics against which control methods could be evaluated (Chapter 5).

## THE STUDY AREA

The study was conducted in a large stand of *Typha* growing on the margins of Rondevlei, a 47.5ha freshwater marsh with stabilised water level (Chapter 3). The vlei was chosen because the rushbeds lay within a bird sanctuary where public access was restricted, thereby minimising the chance of disturbance in experimental areas.

Rondevlei Bird Sanctuary lies approximately 25km south of Cape Town, on the eastern side of the Cape Flats. The climate, geology and vegetation of the area has already been described (Chapter 3). During the study period (September 1987 - August 1989), local air temperatures ranged between 4.0 and 37.7°C (Rondevlei records). Mean annual rainfall at the Sanctuary is 635mm, but was lower during 1988 (521mm: Rondevlei records).

The vlei is a shallow depression formed in calcareous sand with an underlying granite base. Its catchment, is covered by high-density urban development and most of the original Strandveld vegetation has disappeared. The chemistry of the vlei has been described as typical of a shallow well-mixed eutrophic water body (Gardiner, 1988).

The littoral vegetation of the vlei is dominated by *Typha*. The bulrush stands virtually surround the vlei and extend from its damp edges into the water to a maximum depth of 1.2m (Middlemiss, 1974). Areas free of *Typha* are colonised by *Paspalum vaginatum*. *Scirpus littoralis* is common in deep-water areas (Fig. 4.1). Most of the *Typha* stands are monospecific, but landward edges of the southern stands are being invaded by *Senecio halimfolius*.

## METHODS

Demographic methods, calibrated against data collected

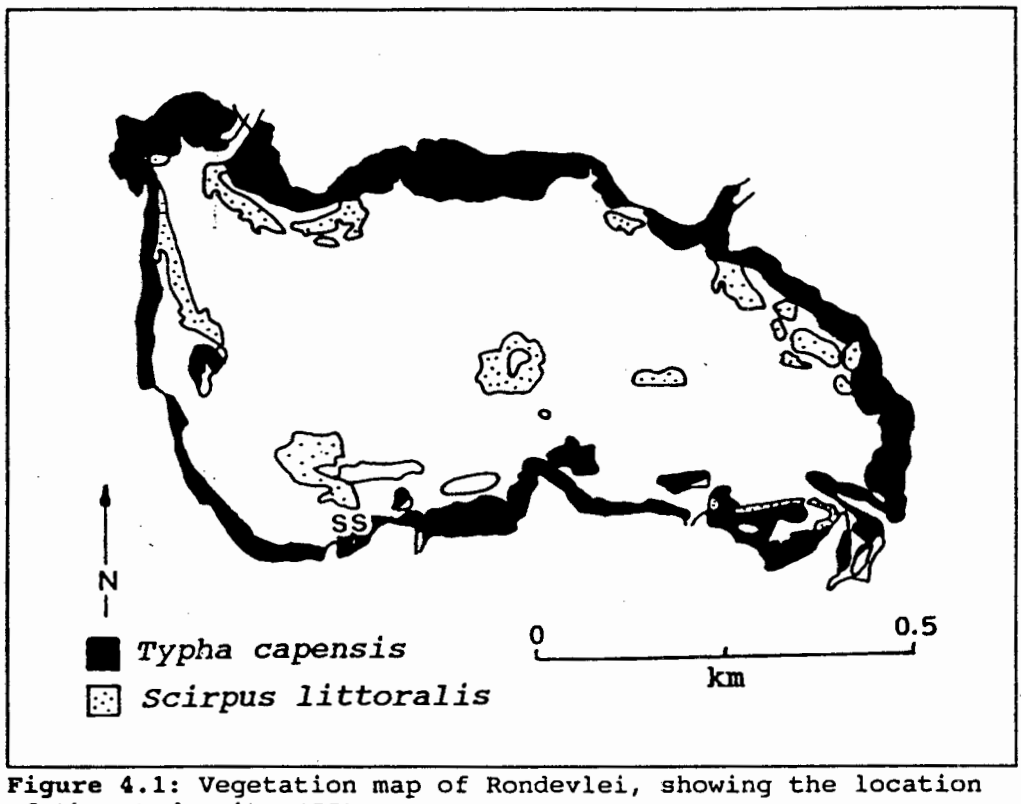



**Figure 4.1:** Vegetation map of Rondevlei, showing the location of the study site (SS).

using harvesting techniques, were used to study the demography, phenology and productivity of *Typha*. All measurements were made from a single rushbed located on the vlei's south-eastern shoreline (Fig. 4.1), chosen because it appeared to be typical of local stands. These are monospecific, and extend across the width of the littoral zone so that different parts are subject to different degrees of inundation. The stand was large enough (40 x 27m) to provide all the harvest material required for this study, leaving enough of the stand undisturbed for demographic measurements.

At the start of the study the general structure of the rushbed was investigated by examining the relationship between stand structure and flood regime. Shoot density, and the relative proportion of live and senescent shoots to standing litter, were estimated within $1m^2$ quadrats placed along ten transects laid through the rushbed at right angles to the shore. Water depth (above or below the soil surface), was measured at 1m intervals along each transect. When the water table fell below ground level, a stainless steel soil corer (10cm diameter) was used to make a

hole 50cm deep, which was then left to fill for 15mins, before the distance between water and ground surfaces was measured. These data were used to plot the shape of the shore profile. Historical water level data (Rondevlei records) were then used to estimate the extent of flooding through the stand.

Phenological and life-history changes where monitored using the methods described by Hultgren (1988). Permanent quadrats ($1m^2$) were set up using a stratified random design, with five replicate quadrats along:

1. the landward edge;
2. the central part of the stand, and
3. the waterward edge.

All shoots (live and dead) within each quadrat were identified by attaching numbered tags to the leaf bases. Maximum shoot heights, measured as the length of the longest leaf from the sediment surface, leaf number and status (live, senescent or dead), and flowering status (already flowered, bud formation, anthesis, seed formation or seed dispersed), were recorded for every shoot. Shoot number (live, senescent and dead), recruitment, death and disappearance were also recorded in each quadrat. This process was repeated over a period of two years, monthly in winter and fortnightly in summer, during which time new shoots emerging were tagged for inclusion in the samples.

To facilitate comparison of shoots emerging during the same period, but under different flood regimes, all marked shoots were assigned to cohorts. Live shoots that were already established at the start of the study were assigned to 50cm size classes according to their height at the first sampling period. The validity of this assignment was tested by comparing height frequency distribution of each cohort for each subsequent sampling occasion (Kolmogorov-Smirnov, Two-sample test). The groups which were significantly different from their closest size class on every occasion ($p<0.05$), were considered to be major

cohorts. Cohorts were numbered according to their apparent order of appearance: Cohort 1 - shoots in the >300cm class, cohort 2 - shoots between 250 and 300cm, etc. Shoots present at the start of the study were divided into a total of 6 cohorts:

C1. >300cm,
C2. 250 - 299cm,
C3. 200 - 249cm,
C4. 100 - 199cm,
C5. 50 - 99cm,
C6. 0 - 49cm.

Shoots produced during the study were grouped according to the number of emergence peaks recorded for each flood regime. Another six cohorts were identified in both the "never-flooded" and "always-flooded" areas, while an extra eleven cohorts are described in the "seasonally-flooded" zone.

The use of different plant modules to describe demographic trends was compared using a subsample of marked shoots from the never-flooded area. The leaves of 50 shoots were individually numbered using permanent marker ink. The status of each leaf (newly produced, starting to senesce, completely senescence or abscised) was recorded on every sampling occasion, and new leaves were numbered as they were produced. The demographic development of these shoots was followed for 12 months.Time constraints prevented the extension of this aspect of the study to the second season, or to other areas within the rushbed.

During the first year, no seedlings appeared in the permanent quadrats, making it impossible to monitor the development of shoots from seed. To ensure that seedlings were included in the sample during the second year, eight $0.5m^2$ permanent quadrats were established in cleared areas in the seasonally-flooded and in the never-flooded zones, where germination had previously been observed. Seedlings germinating in the quadrats were mapped at emergence, and density and

mortality rates were monitored at fortnightly intervals for four months during spring and summer.

Shoots from outside the permanent quadrats were harvested at monthly intervals. All shoots within five randomly selected 0.5m$^2$ quadrats were measured (height, leaf number and status), before all aboveground (AG) material was harvested at ground level. Belowground (BG) biomass was estimated from rhizome biomass following the recommendations of Schubauer & Hopkinson (1984). Rhizomes were retrieved by excavating the sediment below the cleared quadrat to a depth of 50cm. On return to the laboratory, the two fractions were subsampled to determine dry mass by drying to constant mass at 60°C. The ratio of BG:AG biomass was calculated.

Data collected by measuring and harvesting shoots were used to develop a model from which AG phytomass (referred to here as biomass) could be estimated from demographic data. Various linear and non-linear models were tested using step-wise regression of AG biomass against various combinations of shoot height, total leaf number and the number of live, senescent and dead leaves. Belowground biomass was estimated monthly using the ratio of BG:AG biomass calculated as described above.

Net annual aboveground production (NAAP) was calculated using the Allen Curve Method recommended for *Typha* (Dickerman *et al.*, 1986) while net annual belowground production (NABP) was calculated using the Maximum-Minimum Method of Westlake (1975). Net annual production (NAP) was the sum of NAAP and NABP corrected for rhizome mortality (5% - McNaughton, 1975), and for the translocation of energy stores from the shoot to the rhizome during winter die-back (Roberts & Ganf, 1986). *(Methods described on page 165)*

The results from this study are generally presented as the mean of the five quadrats $\pm$ one standard error.

Means were compared using the Mann-Whitney U-test, which assumes that samples are not independent (Siegal, 1956). Differences in variance were tested using the Kruskal-Wallis test (Siegal, 1956), height frequency data from the different areas were compared using the Kolmogorov-Smirnov, Two Sample test (Siegal, 1956). Where other statistical tests were applied, these are noted in the text.

## RESULTS

### STAND STRUCTURE

On the basis of flooding regime the bank colonised by *Typha* could be divided into three zones (Fig. 4.2). The landward zone was defined as the area which was never flooded. Here the sediments were never saturated, although soil moisture rose to a maximum of 42% during winter. The central part of the littoral was flooded to between 2 and 56cm for part of the year (usually from June to December). The upper edge of this seasonally-flooded zone was set at the point where soil became saturated at peak water level. The area along the waterward edge of the stand was always flooded and here the sediments were permanently inundated to a minimum depth of 1cm.

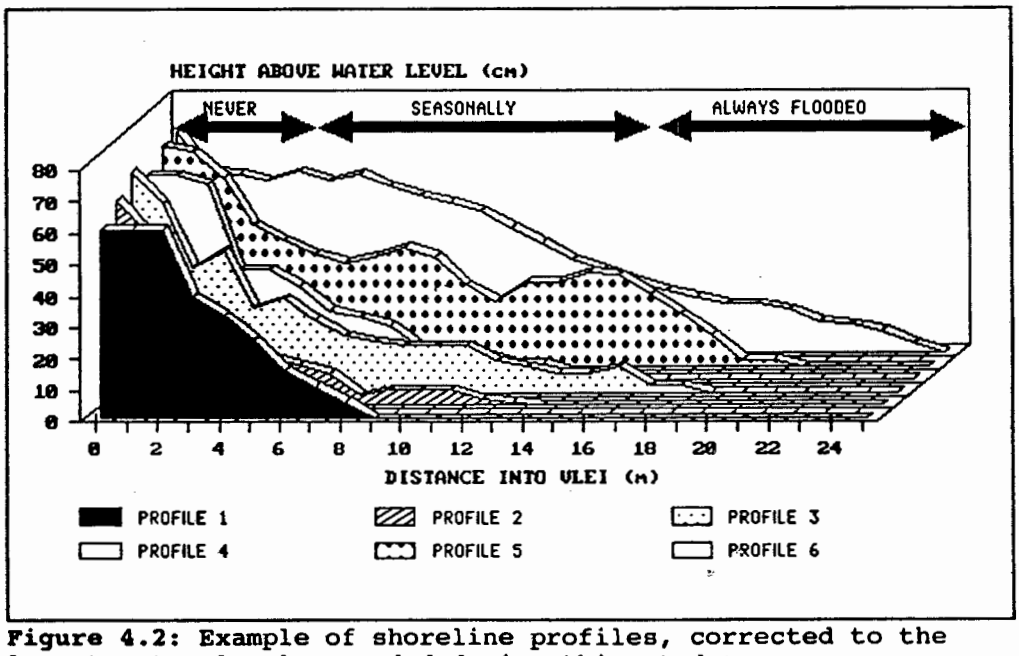



**Figure 4.2:** Example of shoreline profiles, corrected to the lowest water level recorded during this study.

Shoots of all sizes and life stages were recorded within the study stand. New or juvenile shoots were shorter and had fewer leaves than generative shoots, but both groups were composed of predominantly chlorophyllous leaves. Tall (>1m) chlorophyllous shoots were considered to be capable of reproduction (generative shoots), but died soon after flowering (becoming standing litter). Dead shoots which had not flowered were also found in large numbers. Until completely dead (0% chlorophyllous), these were 'classed as generative.

The density of shoots, and the relative number of shoots from different life-stages, varied along the width of the rushbed and could be used to divide it into four areas with different growth phases (Table 4.1). Shoot densities in both the landward and the central part of the rushbed were high, and included few juveniles, but their demographic structure varied. Generative shoots dominated the central part of the stand (generative growth phase) while standing litter was abundant along the landward edge (senile growth phase). Along the eastern edge of the stand, where shoots were colonising a mudflat area, shoot density decreased and juvenile shoots became more abundant (invasive growth phase, open). Shoot density in this area was similar to that along the waterward edge of the stand, but generative and juvenile shoots were present in approximately equal numbers (invasive growth phase, flooded).

A strong relationship between stand structure and flooding regime was identified (Fig. 4.3). The senile phase lay in the never-flooded area, while generative shoots were typical of areas which were seasonally-flooded. The invasive phase was confined to the always-flooded area and the uncolonised littoral zone, areas into which the stand was spreading.

**TABLE 4.1:** Variation in stand composition within a single rushbed. $\bar{x}$ - mean; se - standard error; juvenile shoots - shoots not yet capable of reproduction; generative shoots - mature shoots capable of reproduction; senile shoots - shoots no longer capable of reproduction.

| RUSHBED STRUCTURE | MATURE | | | | INVASIVE | | | |
|---|---|---|---|---|---|---|---|---|
| | SENILE | | GENERATIVE | | OPEN | | FLOODED | |
| | $\bar{x}$ | se | $\bar{x}$ | se | $\bar{x}$ | se | $\bar{x}$ | se |
| Shoot density (shoots $m^{-2}$) | 24.6 | 3.7 | 36.2 | 5.2 | 11.2 | 3.8 | 8.8 | 4.1 |
| Proportion (%) of Total Population being: | | | | | | | | |
| Juvenile shoots | 0.0 | | 5.2 | | 97.9 | | 47.5 | |
| Generative shoots | 42.4 | | 82.6 | | 2.1 | | 50.9 | |
| Senile shoots | 57.6 | | 12.2 | | 0.01 | | 1.6 | |

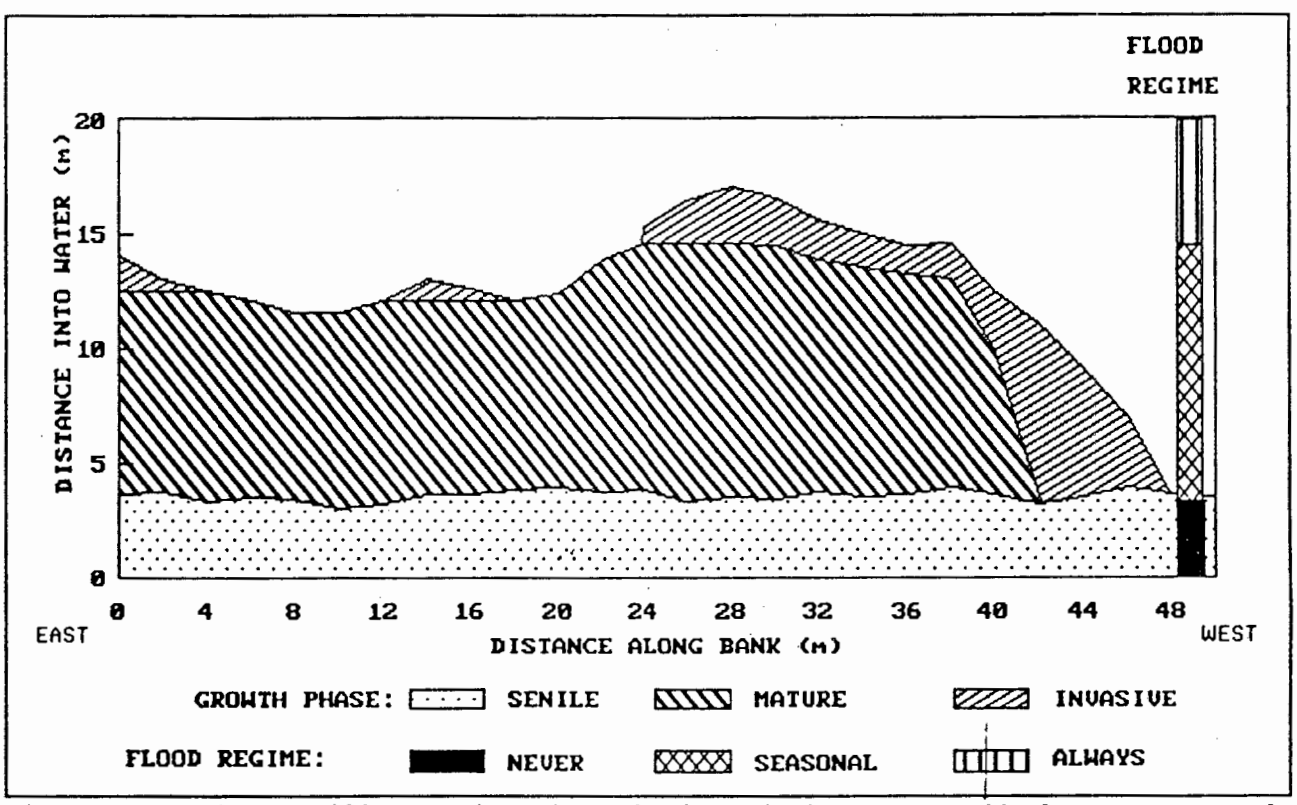



**Figure 4.3:** Diagram illustrating the relationship between rushbed structure and flood regime.

**PHENOLOGICAL DEVELOPMENT**

Seedlings were only recorded between September and December. They appeared on damp sand and exposed mud flats as a dense mat. They were never found in areas where shoots were already established.

Seedling density ($96m^{-2}$ ± 4.6) and establishment success (12.9% ± 4.1) were lowest in the never-flooded zone. In the seasonally-flooded area, where seedlings were more abundant ($114m^{-2}$ ± 12.7), the rate of successful establishment was higher (24.5% ± 3.6). After drawdown, however, seedling mortality rose from 56 to 97% $wk^{-1}$. Mortality was highest among the youngest seedlings, suggesting that death was related to seedling age at drawdown as well as to changes in water supply.

Emergent shoots, the product of rhizome elongation, were easily distinguished from seedlings by their first leaves, which were vertically rolled (the bud sheath). They appeared throughout the year, but emergence peaked between September and November (Fig. 4.4a).

During the first month of growth leaves were produced by new shoots at a mean weekly rate of 2.1 $shoot^{-1}$, and only the sheath leaves were abscised. Leaf elongation rates varied between 11.5 and 71.5mm $d^{-1}$. During the next five to twelve weeks leaf number varied widely since production and abscission were unsyncronised, but by the end of this period of establishment shoots had an average of 8 leaves $shoot^{-1}$ ± 2.1, and leaf abscission rates ($0.99 shoot^{-1} week^{-1}$ ± 0.12) mirrored the rate at which leaves were produced.

The rate of leaf elongation declined to 2.8mm $d^{-1}$ ± 0.4 between February and July, irrespective of shoot age. During this period the leaf tips of most shoots senesced. As air and soil temperatures rose (August and September), these shoots underwent a second growth

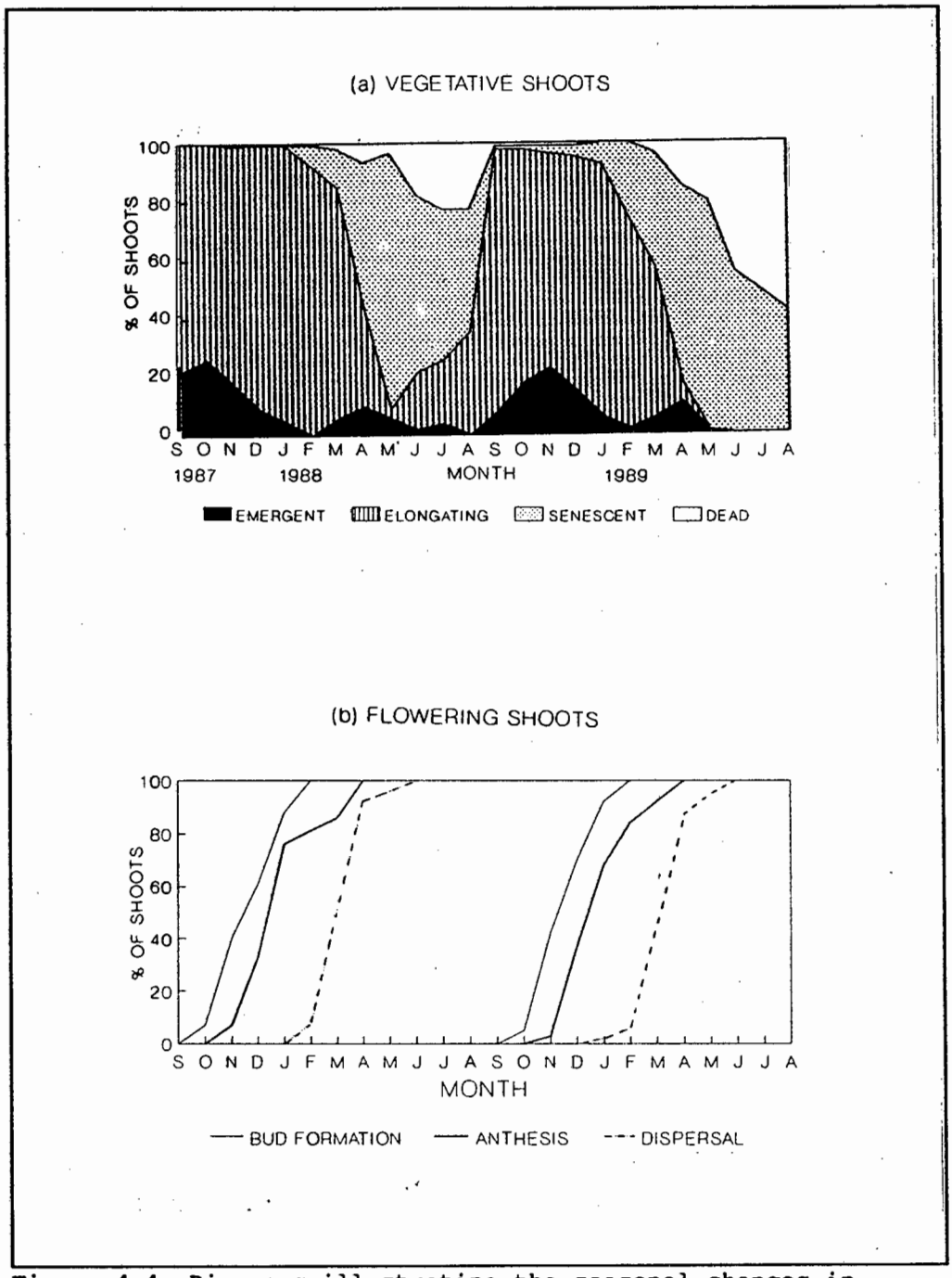



**Figure 4.4: Diagrams illustrating the seasonal changes in phenology in (a) vegetative shoots and (b) flowering shoots.**

phase which extended into January; mean rate of elongation was 6.1mm $d^{-1}$ ± 0.1. The number of new leaves produced during the second growth phase exceeded the rate of leaf abscission, and leaf number increased to a maximum of 20shoot$^{-1}$ ± 2.1.

Most flowering shoots (86%) were in their second season of growth. Bud formation began in October and continued until January, with a peak in November (Fig. 4.4b). The terminal male spike ripened first and shed its pollen three weeks after its appearance (December - January). Seed heads were present from January to June, but most were dispersed during February, when conditions were dry and windy. Relatively few (15% ± 2.4) generative shoots flowered.

The most obvious difference in phenological development between the shoots growing under the different flood regimes was the difference in timing of emergence (Fig. 4.5). In all areas most new shoots appeared in September and October, but the number of emergent shoots varied between flood regimes. Furthermore, in flooded areas, new shoots appeared throughout the year (Fig. 4.5 a,b), but in the driest zone most new shoots appeared between July and November (Fig. 4.5c).

The proportion of shoots in different life-stages also varied between shoots under different flood regimes. Senescent shoots were usually recorded throughout the year in the never-flooded zone, but were only present in the flooded areas during winter. Dead shoots were most abundant in the always-flooded zone during the first winter of the study, and the proportion of dead shoots during winter was similar between years: 48% in 1988; 46% in 1989 (Fig. 4.5a).

In the seasonally- and never-flooded areas, the proportion of dead shoots was considerably less during the first winter than during the second: 16% in 1988, 47% in 1989 in the seasonally-flooded zone (Fig.

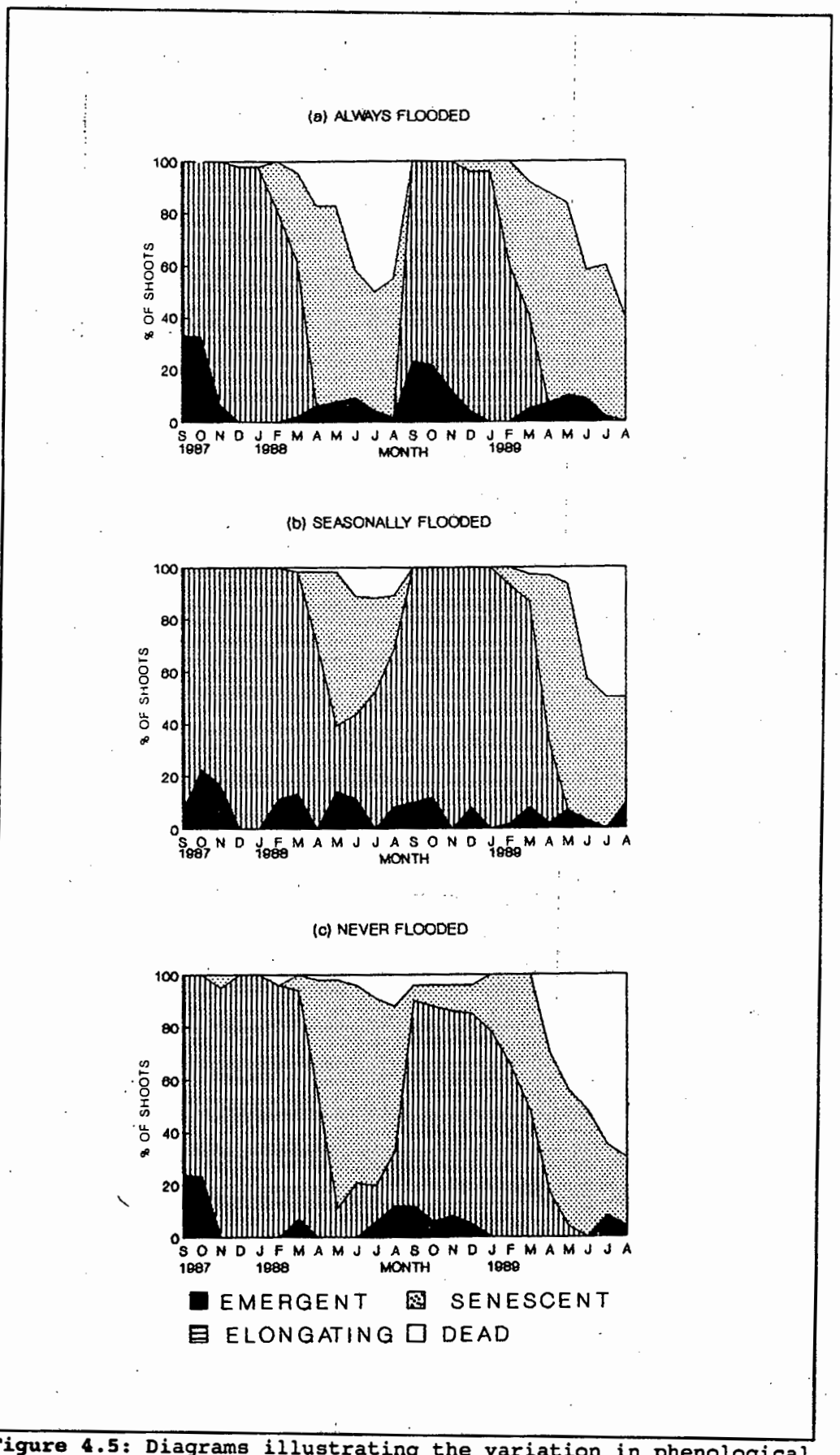



**Figure 4.5:** Diagrams illustrating the variation in phenological development between shoots growing under different flood regimes.

4.5b), 11% in 1988 and 73% in 1989 in the never-flooded zone (Fig. 4.5c).

## DEMOGRAPHY

### Emergence and Cohort Structure

Emergence rates peaked during spring (September - October) in all zones, but new shoots were produced throughout the study period in all except the driest zone (Fig. 4.6). In the never-flooded area recruitment stopped during summer, suggesting that it was limited by lack of water.

The number of shoots emerging in each quadrat was extremely variable (coefficient of variation lay between 80 and 124%), so total emergence in each area (the sum of emergence in five quadrats) is reported (Fig. 4.6). Under all flood regimes recruitment was greater during the first season. For example, 280 new shoots were produced during one year in the seasonally-flooded area, but in the following year recruitment fell 37%, to 188 new shoots. Recruitment was lowest under always-flooded conditions: 170 new shoots in 1987/88, 127 new shoots in 1988/89.

The pattern of shoot emergence also varied with flood regime. In the never-flooded zone, emergence peaked in July, in September, and again in November and December, producing three cohorts each year. In 1988, a small cohort was produced in March, but there was no similar cohort recorded the next year (Fig. 4.6c). Emergence in the always-flooded areas was similar in that three cohorts were produced each year, but these were produced during October, in December and then from February to June (Fig. 4.6a). In the seasonally-flooded area, five cohorts were produced each year, at approximately two monthly intervals (Fig. 4.6b).

The size of the cohorts emerging from the different

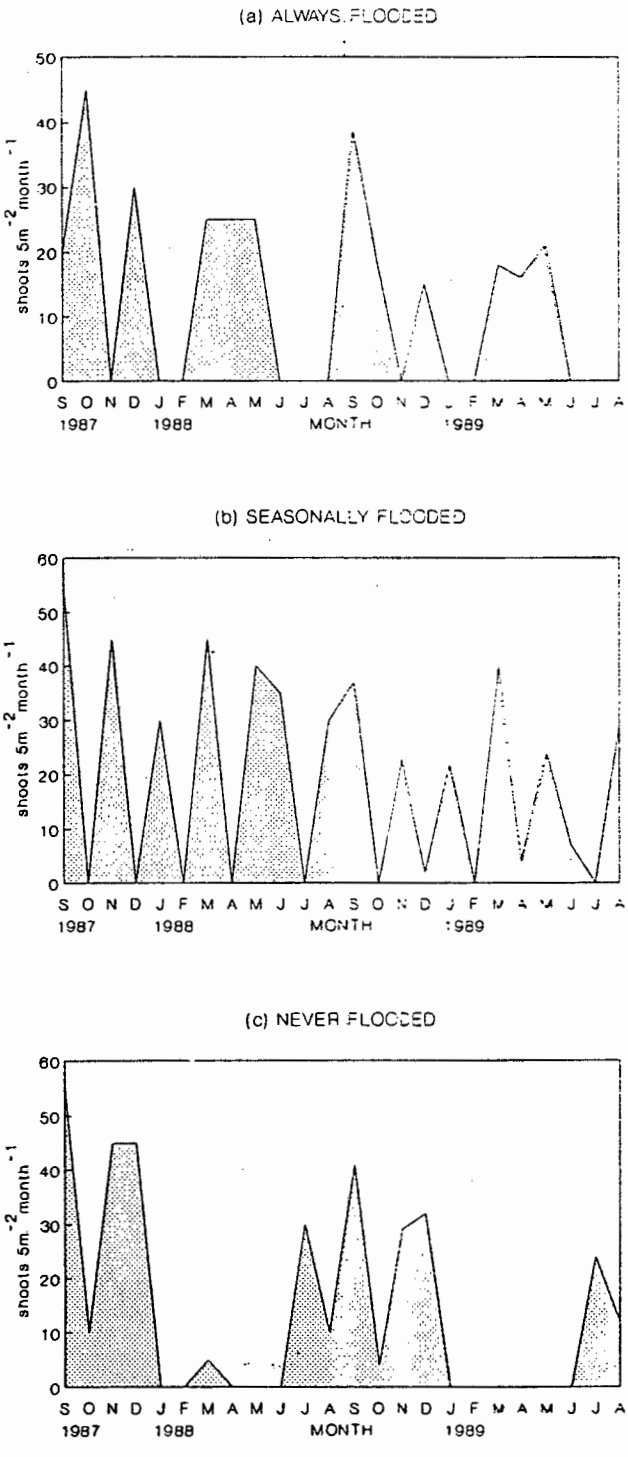



**Figure 4.6: Diagrams showing the variation in shoot emergence under different flood regimes.**

areas varied. The first spring cohort was relatively large in the never- and seasonally-flooded areas (55 shoots) compared to that of the always-flooded area (20 shoots). The relative size of cohorts emerging between March and May was similar: 40 to 45 shoots $month^{-1}$ in the seasonally-flooded area and 25 shoots $month^{-1}$ in the always-flooded area (there was no late summer cohort in the never-flooded area).

**Shoot Mortality**

Shoot mortality in the always- and seasonally-flooded areas peaked during the winter months, but was aseasonal in the never-flooded zone (Fig. 4.7). Mortality rates were always highest in this area, varying between 8 and 95 shoots $5m^{-2}$ $month^{-1}$. Maximum mortality in the always- and seasonally-flooded areas peaked at 73 shoots $5m^{-2}$ $month^{-1}$.

Mortality rates in all areas were higher during the second year of study. The increase was similar in the never- and seasonally-flooded areas, where mortality rose from 295 to 400 shoots $5m^{-2}$ $yr^{-1}$ and from 230 to 320 shoots $5m^{-2}$ $yr^{-1}$ respectively. This increase was approximately half that recorded in the always-flooded area, where mortality increased 15%, from 305 to 360 shoots $5m^{-2}$ $yr^{-1}$.

Mortality was highest amongst shoots in their second season (cohorts 1 to 5), being between 100 and 85% of C1 and C2 shoots respectively. Mortality among C3, C4 and C5 was lower, especially in the wet areas, where only one third of these shoots died. In the never-flooded area between 36 and 52% of these shoots died in their second season.

Mortality was not, however, restricted to shoots in their second year of growth. In the seasonally-flooded area, 25 to 32% of C7 shoots died during their first summer. In the never-flooded area between 25 and 50% of shoots from C6, C7 and C8 died during the

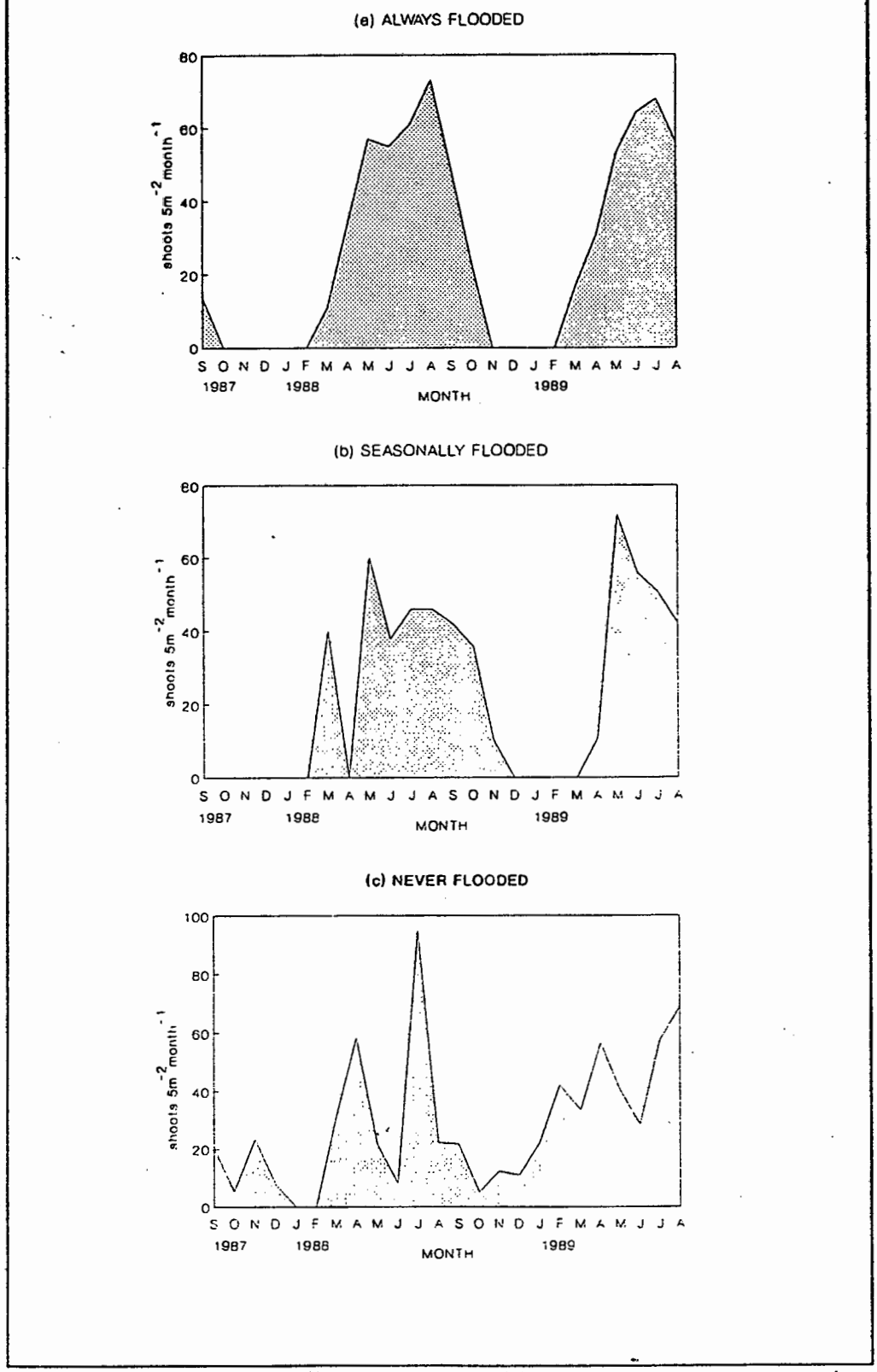



**Figure 4.7**: Variation in shoot mortality amongst shoots growing under different flood regimes.

same period.

Juvenile mortality was lower than that of the generative shoots. It was only recorded in the never-flooded area, where 10% of newly emerged shoots died within two months of emergence. Dickerman (1982) found that most juvenile mortality occurred within one week of emergence. If mortality was similar in the study population, then juvenile mortality may have been under-estimated by fortnightly sampling.

**Survivorship**

The probability of shoot survival was calculated for each cohort as the percentage of shoots surviving from one sampling period to the next. Survivorship curves for cohorts 1 (the oldest shoots), 3 (assumed to be shoots from the previous season), and 6, 7 and 8 (the first cohorts emerging during this study) are presented to illustrate shoot survival over as wide a period as possible (Fig. 4.8). The staircase-type curves for all cohorts, in all areas, indicate that survivorship changed abruptly as shoots moved from one life-history stage to another.

The probability of survival amongst C1 shoots from all areas fell dramatically during the winter of 1988. In contrast, that of C3 shoots remained relatively high during the first season, but fell to zero in the second winter in the seasonally- and never-flooded areas.

Survivorship of cohorts 6, 7 and 8 in the never-flooded area was generally lower during all life stages than in the wetter areas. This was particularly so during the juvenile stage, when the probability of survival fell markedly within two months of emergence, after which survival potential decreased more slowly.

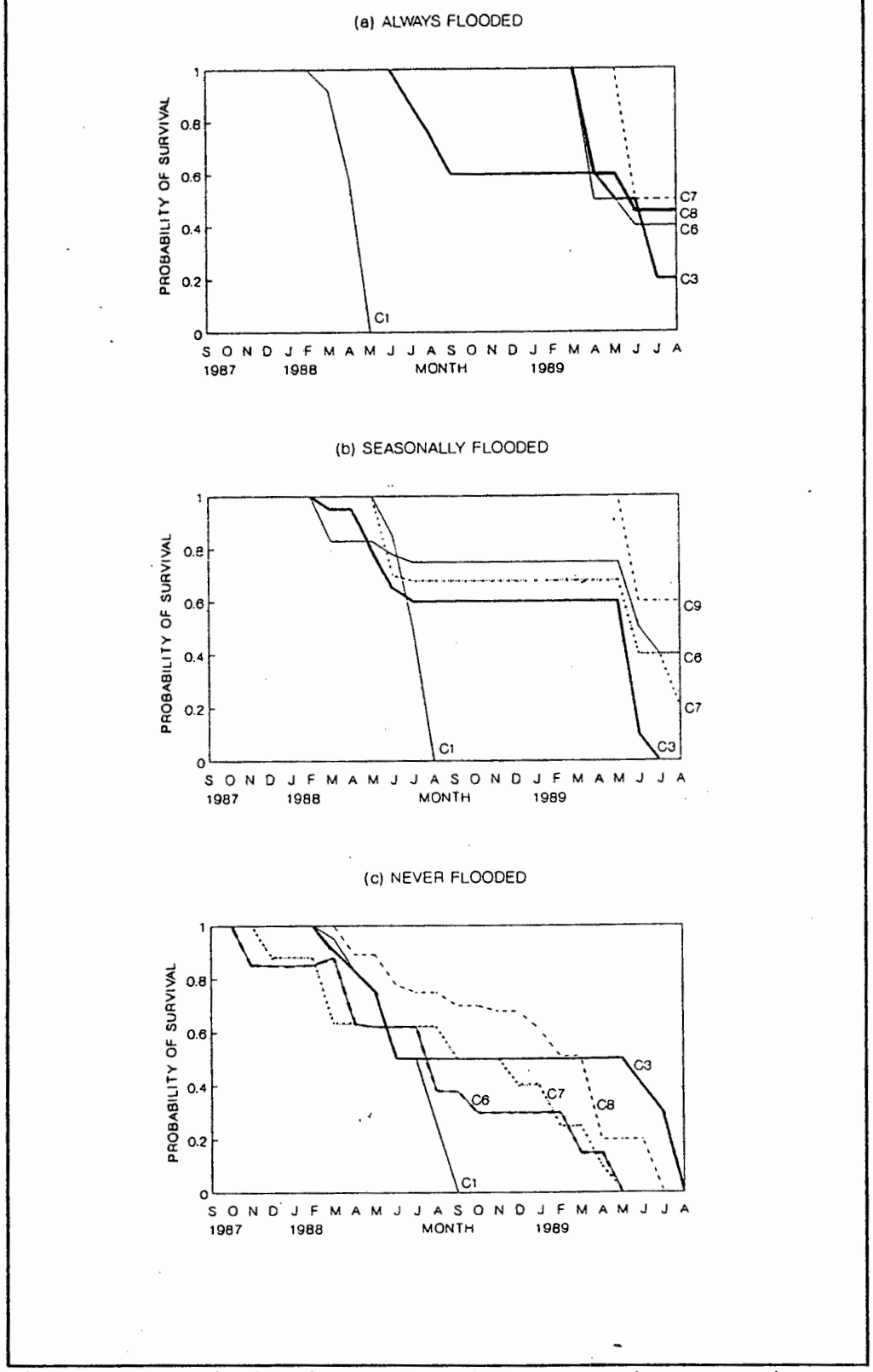



**Figure 4.8:** Variation in surviorship amongst shoots growing under different flood regimes.

In the seasonally-flooded area the probability of survival amongst cohorts 6, 7 and 8 decreased during winter, but remained constant during the summer months. None of the cohorts was eliminated during the study period, indicating that most seasonally-flooded shoots lived for longer than two years.

Survivorship of cohorts 6 to 8 was highest in the always-flooded area, and all shoots survived their first winter. The probability of survival only decreased at the onset of their second winter period, when approximately half the shoots died. Shoot longevity was less than that of seasonally-flooded shoots, but some shoots survived more than two years.

## SHOOT POPULATION DYNAMICS

### Shoot Height and Growth Rate

Shoot height is largely determined by environmental conditions during the period of shoot emergence and growth (Grace & Wetzel, 1981b), and so it should vary between cohorts, and between flood regimes. Because environmental conditions such as moisture supply change relatively quickly, growth under different flood regimes could only be compared for the cohorts whose date of emergence was known. These are C6 and C7, which were first recorded in September, and between November and December 1987 respectively, and C8 of the never- and always-flooded areas, which were compared to C9 of the seasonally-flooded area. These shoots appeared between February and March 1988.

Shoot height, represented as mean height of each cohort on each sampling occasion, is illustrated in Figure 4.9. The oldest shoots were generally the tallest, but the difference in mean height between cohorts did diminish with time. Mean maximum height was similar in the seasonally- and always-flooded areas: 287.4cm $\pm$ 51.7 and 290.2cm $\pm$ 34.8 respectively.

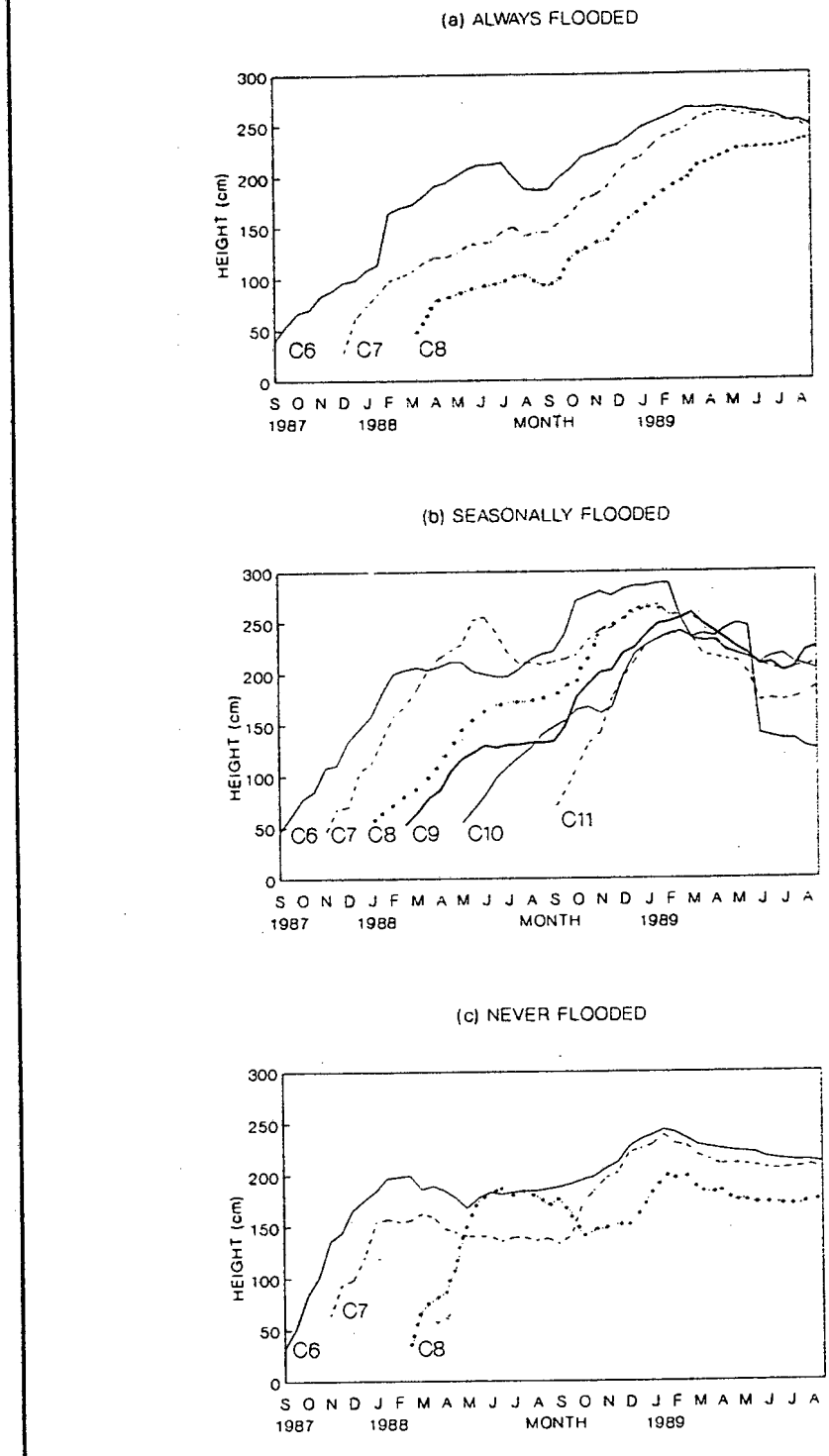



**Figure 4.9:** Mean shoot height, by cohort, under different flood regimes.

The height of never-flooded shoots was significantly less than both seasonally- and always-flooded shoots (Mann-Whitney U-test, $p<0.05$). The trend toward taller shoots being produced in deeper water is typical of emergent species. For example, it has been reported in *Juncus militaris* (Hogeland & Killingbeck, 1985) and *Scirpus maritimus* (Lieffers & Shay, 1982).

Mean shoot height increased most rapidly during early summer in both growth periods, with a lag during the cooler months. This was most marked in the never-flooded area, where growth actually stopped in late summer. Shoots from all cohorts in the seasonally- and never-flooded areas began to die back during the second winter, but in the always-flooded area die-back was only observed amongst cohorts 6 and 7.

Plant height, changes of which reflect growth, increased most rapidly in the never-flooded area (Fig. 4.10). For example, during the first 90 days shoots from C6 grew 97, 134 and 166cm respectively in the always-, seasonally- and never-flooded zones.

The growth period varied between flood regimes, and was longest in the area that was always flooded. This was most apparent among shoots from C7 where growth ceased after 110 and 210 days respectively in the never-flooded and seasonally-flooded areas, but was still increasing after 225 days in the always-flooded area. The longer growth period of the always-flooded shoots meant that mean maximum shoot height was not significantly different from that of shoots from the seasonally-flooded area (Mann-Whitney U-test, $p<0.05$), despite differences in their growth rates.

Variation in the length of the growing period was also observed among cohorts from the never-flooded area. Growth continued for 165, 120 and 105 days for cohorts 6, 7 and 8. This may

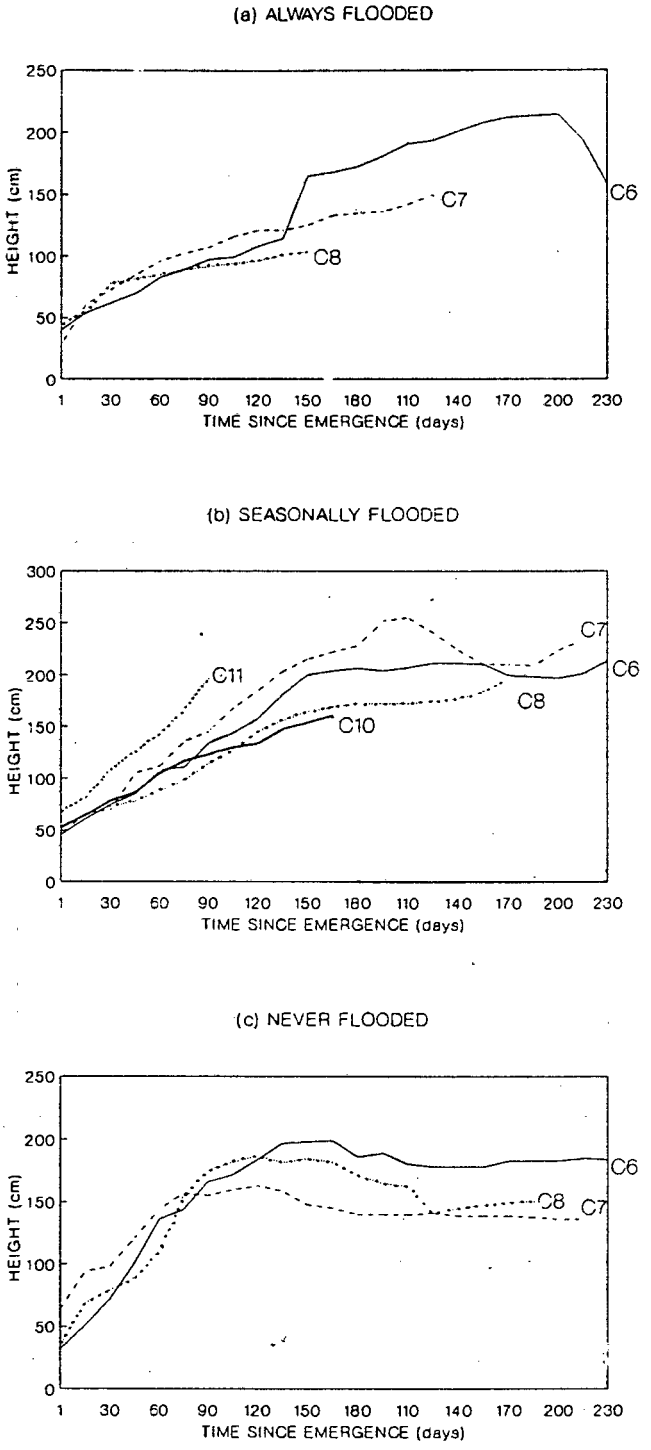



**Figure 4.10:** Variation in growth rate, and growth period of shoots growing under different flood regimes.

partially have been due to differences in climatic conditions because shoots emerging later in the season were subject to longer periods of low temperatures. However, the growth of cohorts 6 and 7 ended prior to the onset of cooler weather, and appeared to be primarily related to drawdown which reduced the water supply of C7 shoots relative to that of C6 shoots.

**Stand Shoot Dynamics**

The proportion of live and senescent shoots to standing litter varied seasonally and with flood regime (Figs. 4.11 - 4.13). Senescent shoots were the dominant component of the always-flooded area during winter, and they persisted during summer (Fig. 4.11). Dead shoots, mainly from the generative class (juvenile shoots may not have been recorded as they may have been below water level), were present between March and September. These shoots did not persist as standing litter.

Live shoots dominated the seasonally-flooded zone for most of the year (Fig. 4.12a). Senescent shoots, mainly from the generative class (Fig. 4.12b & c), were recorded only during the winter die-back period, when they became the dominant shoot class. Standing litter density increased in winter, but was low during the rest of the year. None of the juvenile shoots remained as standing litter, and the number of dead large shoots persisting was reduced by comparison to shoots in the driest zone.

In the driest zone, standing litter made up a relatively large part of the standing crop, except during January and February when the proportion of litter fell to less than 1% (Fig. 4.13). Shoots from both generative and juvenile classes made up standing litter. Senescent shoots, primarily from the generative class, were present throughout the study. This was in contrast to the seasonal appearance of senescent shoots in the seasonally-flooded area.

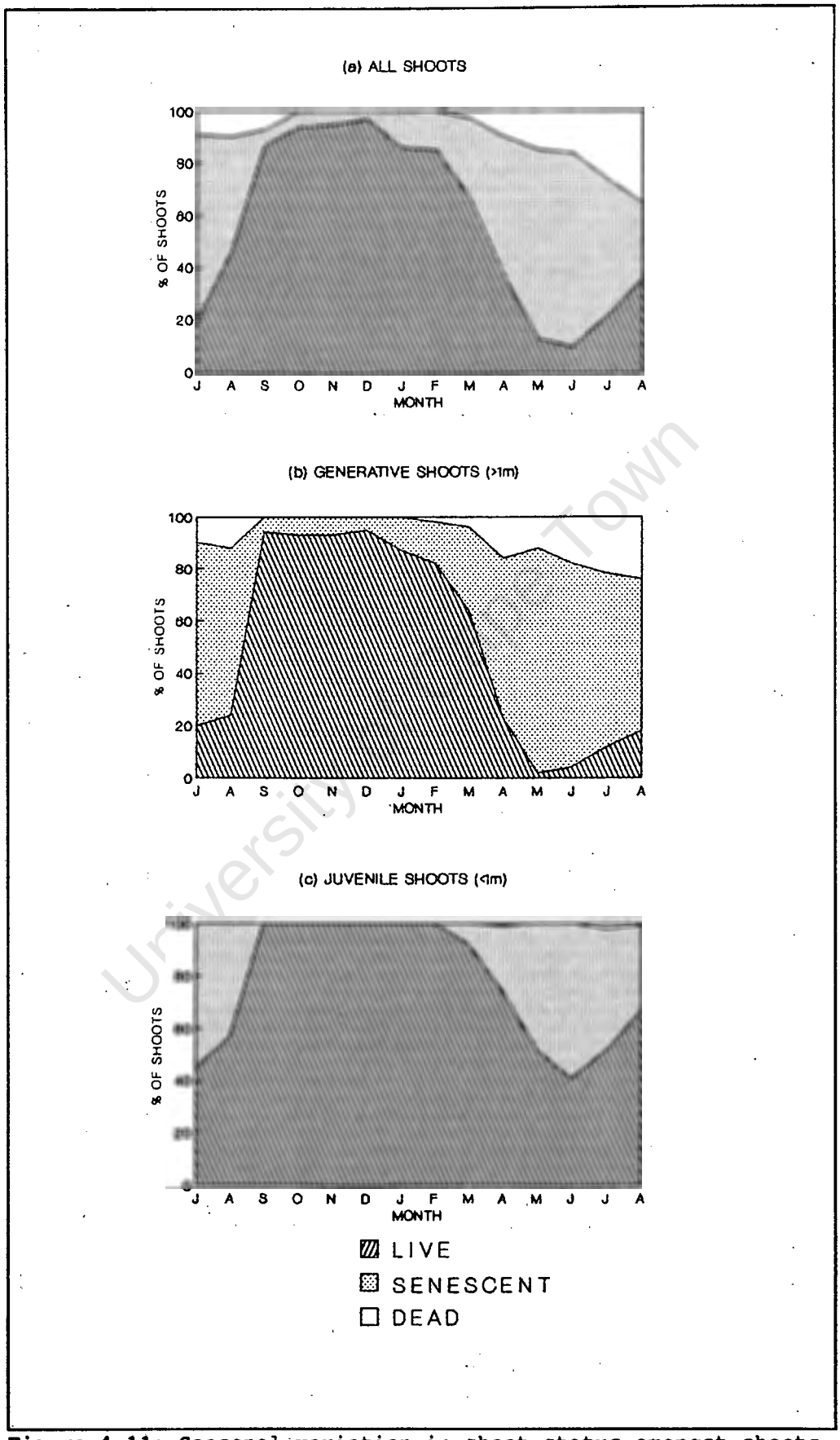



**Figure 4.11:** Seasonal variation in shoot status amongst shoots from the alway-flooded zone.

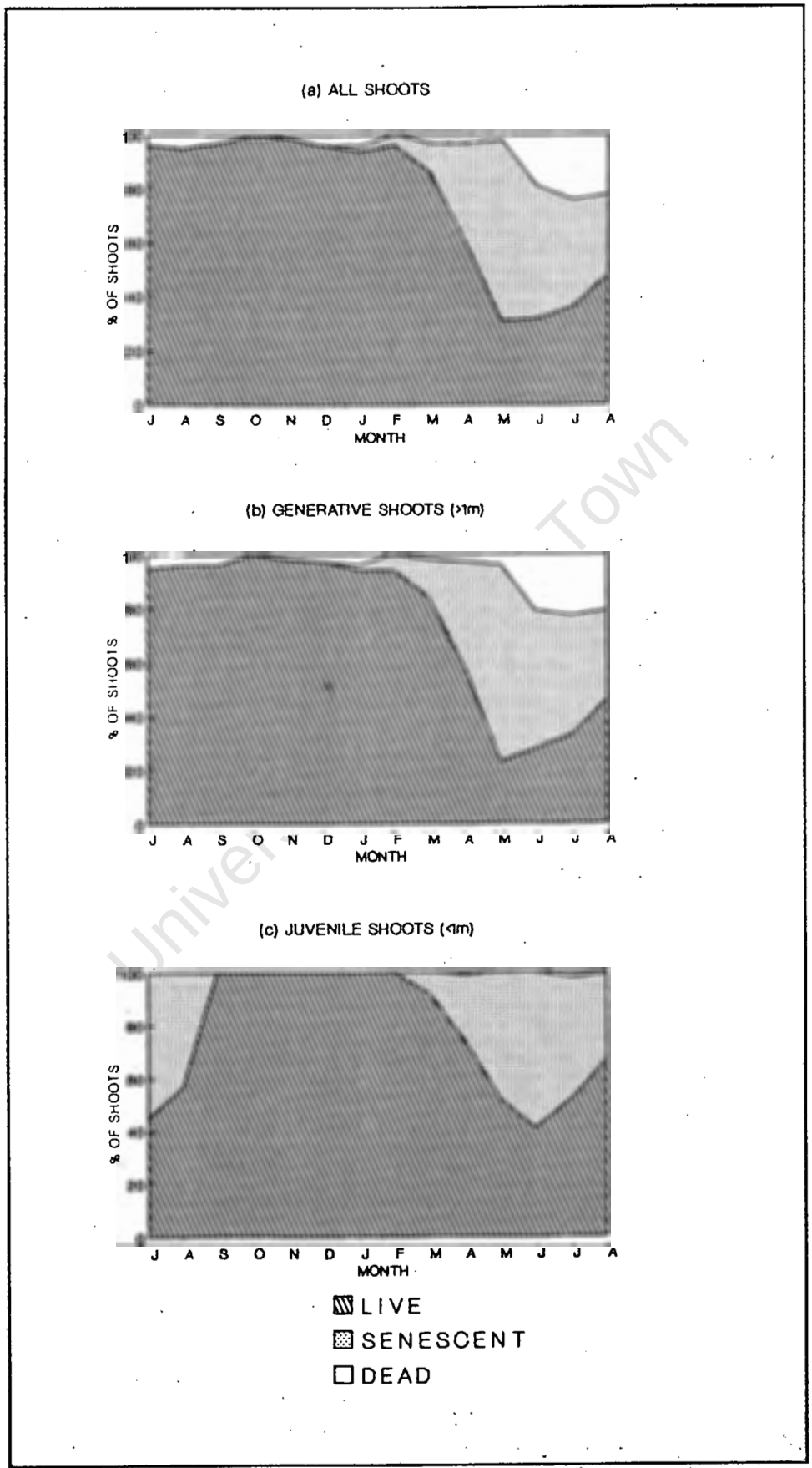





**Figure 4.12:** Seasonal variation in shoot status amongst shoots from the seasonally-flooded area.

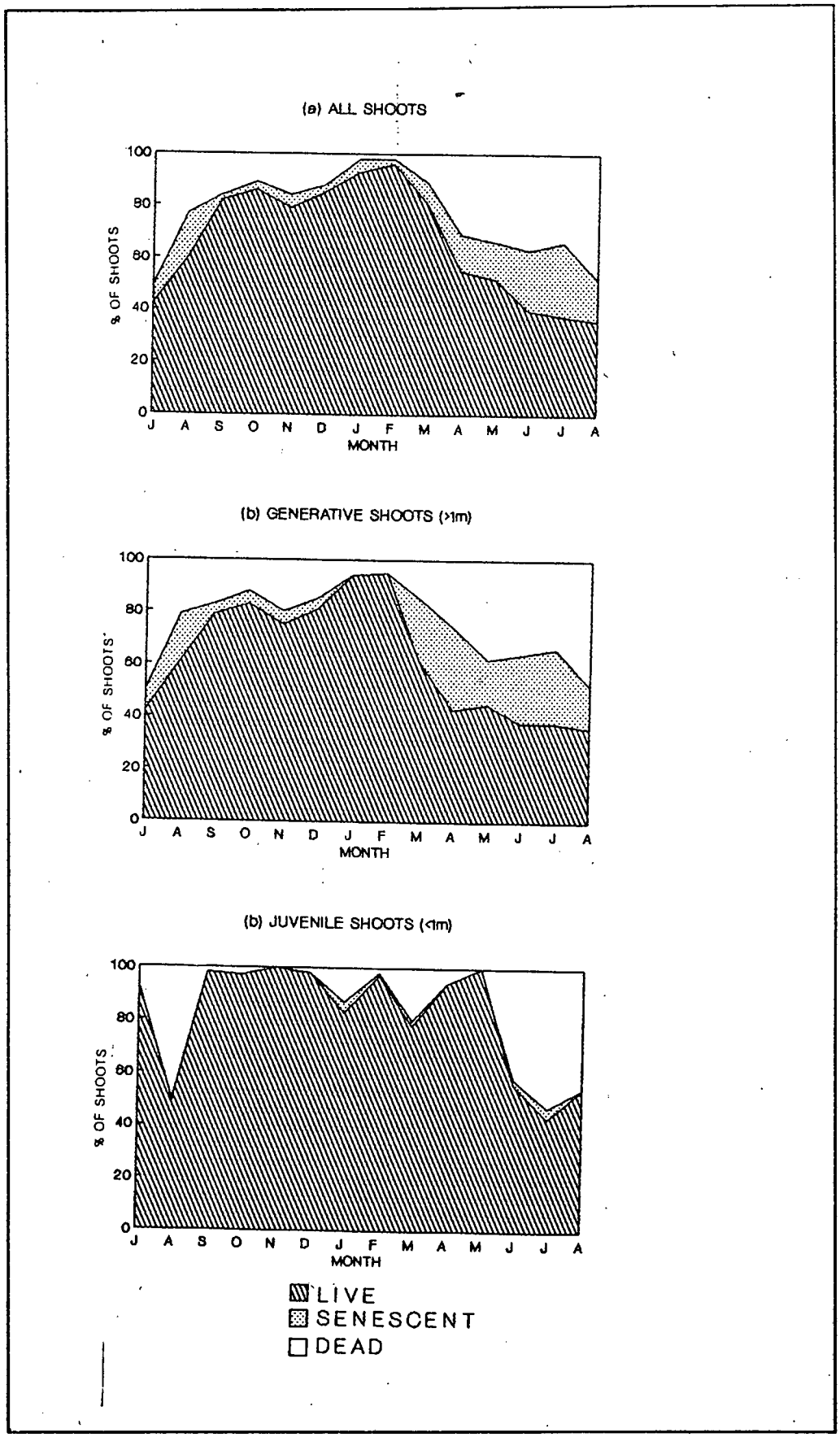



**Figure 4.13:** Seasonal variation in shoot status amongst shoots from the never-flooded area.

**Shoot Density**

Live shoot density varied with flood regime, season and year (Fig. 4.14). Density was lowest in the always-flooded area where it fluctuated between 12.1 and 24.2 shoots $m^{-2}$, peaking in April 1988 and in June 1989. In the never-flooded area, live shoot density varied between 15.0 and 30.2 shoots $m^{-2}$. Maximum density was highest during the second season, although winter minima were similar. Live shoot density was highest in the seasonally-flooded area, where maximum densities of 47.6 and 48.3 shoots $m^{-2}$ were recorded in April 1988 and in July 1989. Live shoot density was lowest in July 1988 (30.7 shoots $m^{-2}$).

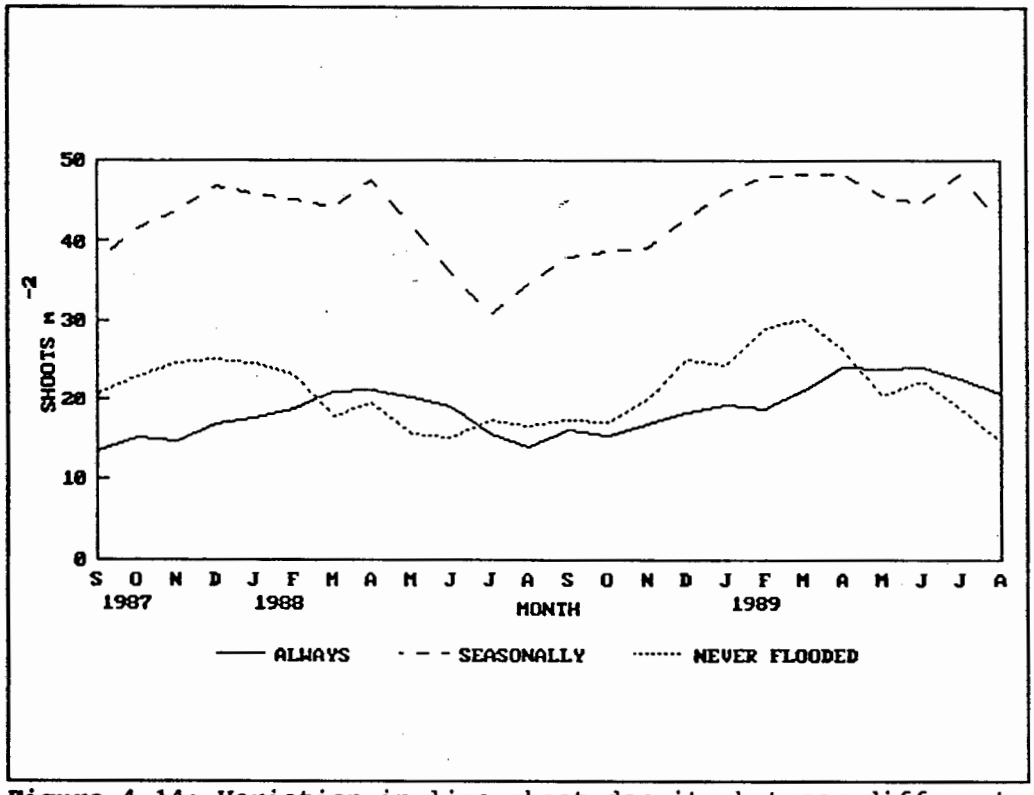



**Figure 4.14:** Variation in live shoot density between different flood regimes.

In the seasonally- and never-flooded areas maximum shoot densities were recorded during December of the first season and between February and March the following year. In the always-flooded area, a similar two month lag was recorded between years, and density peaks were recorded after those observed in the seasonally- and never-flooded areas.

The lag between peak density under the different flood regimes was due to differences in the speed with which shoots became established. Shoot density increased most rapidly among shoots which were never-flooded, particularly during the first season. Maximum density was thus reached early, and was maintained for the rest of the season. The opposite was true in the always-flooded area, where shoot density increased gradually throughout the growing season, peaking just prior to the winter die-back.

The density of dead shoots (standing litter) varied seasonally, peaking during the winter under all flood regimes (Fig. 4.15). Standing litter was always most abundant in the never-flooded areas where a maximum density of 16.4 shoots $m^{-2}$ was recorded. During the study period, standing litter accounted for 22.8% ± 14.4 of total shoot density in this area. This compared with 0.1% ± 0.6 of shoots in the always-flooded area, and 5.5% ± 2.7 in the seasonally-flooded zone.

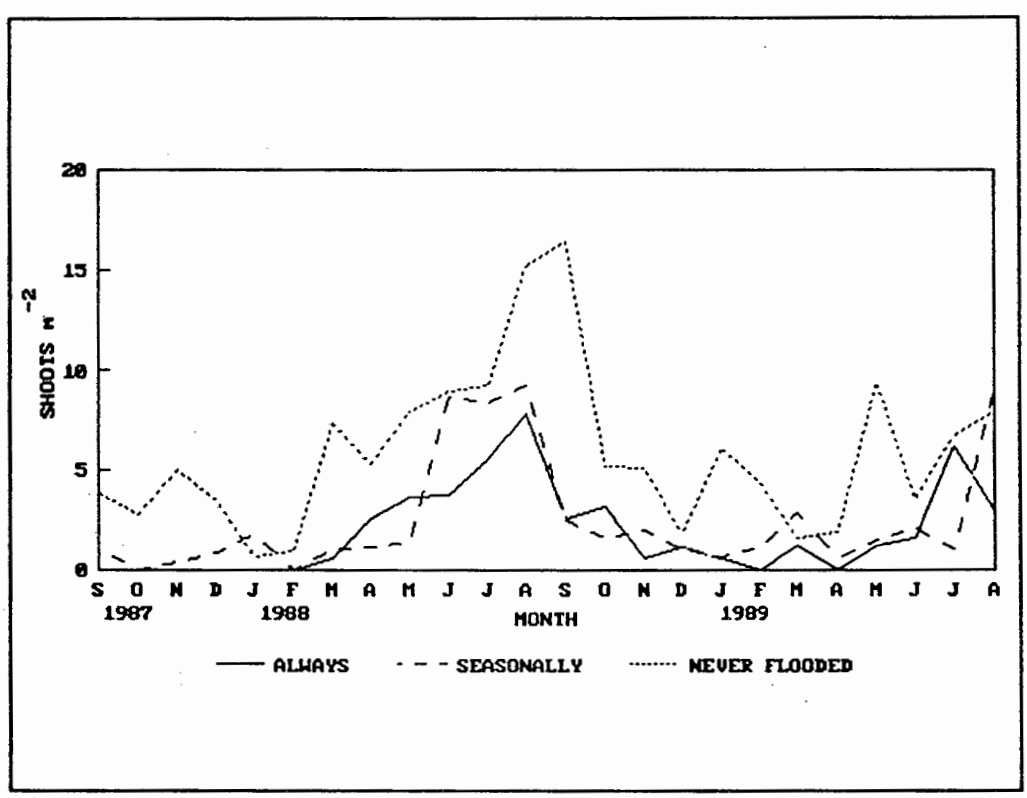



**Figure 4.15:** Seasonal variation in standing litter density between different flood regimes.

## LEAF POPULATION DYNAMICS

### Leaf Production (Recruitment)

The production of new leaves was highest during the month following emergence for all cohorts, despite differences in date of emergence (Fig. 4.16). New leaves were produced most rapidly by C7 shoots with a mean rate of 3.8 week$^{-1}$ being recorded. New leaves were produced throughout the year, but recruitment was generally highest during the summer months.

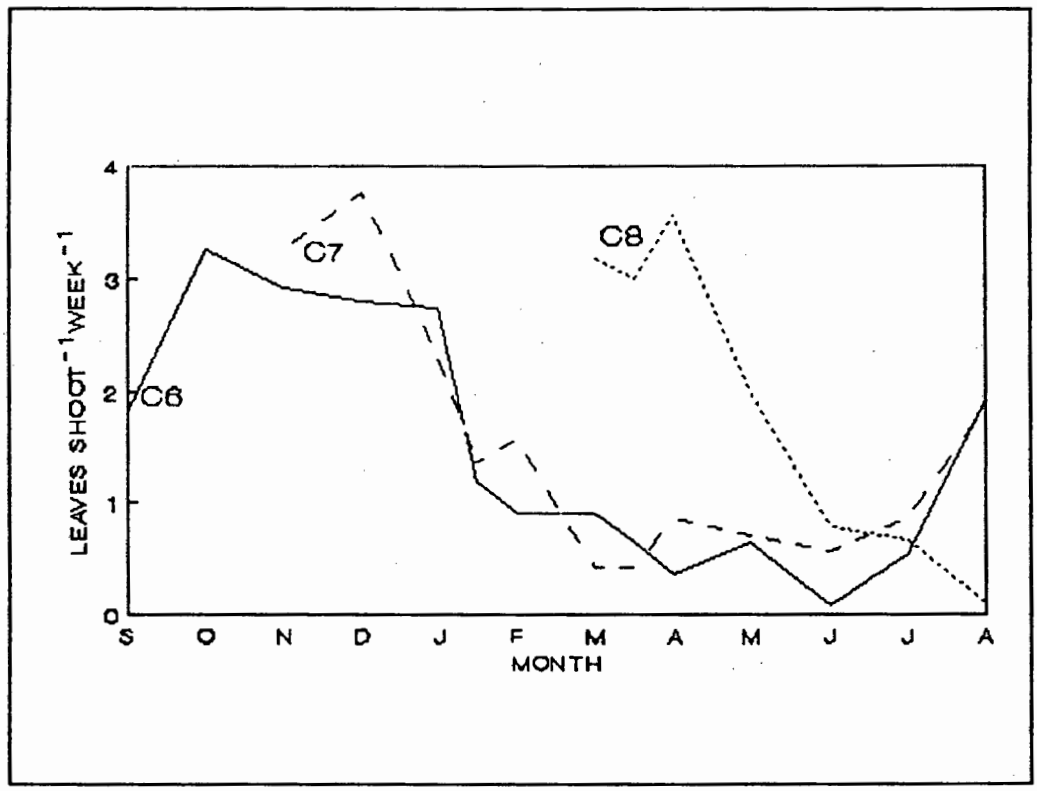



**Figure 4.16:** Leaf recruitment by shoots of different cohorts from the seasonally-flooded zone.

### Onset of Senescence

Leaves began to senesce soon after emergence, but senescence peaked with the onset of the cooler winter months between March and April (Fig. 4.17).

There was no difference in the pattern of leaf senescence between shoots from different cohorts. This suggests that leaf senescence is controlled by environmental factors such as air temperatures, rather

than by leaf size or age.

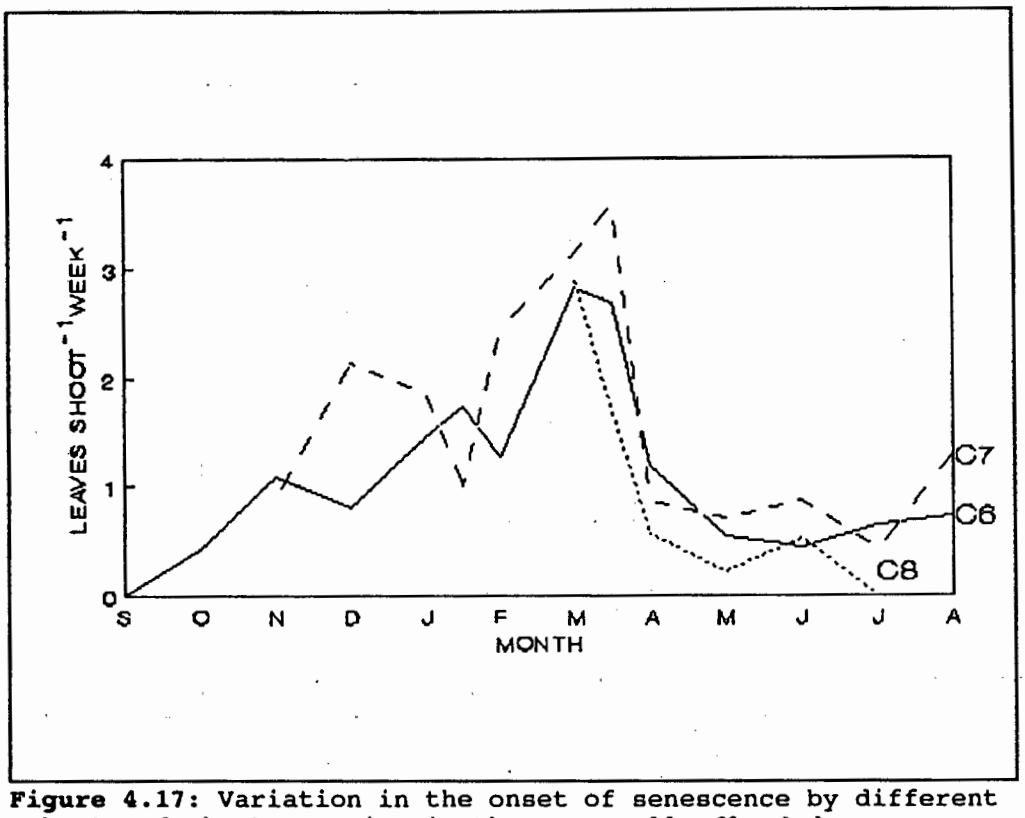



**Figure 4.17:** Variation in the onset of senescence by different cohorts of shoots growing in the seasonally-flooded zone.

**Leaf Death (Complete Senescence)**

Leaf death occurred throughout the year, even in the months immediately following emergence (Fig. 4.18). The rate at which leaves died peaked between March and April in all cohorts. This is the same period over which the onset of leaf senescence reached its peak. This suggests that once leaves began to senesce, death followed relatively quickly.

**Leaf Abscission**

Leaf abscission lagged behind death by approximately one month (Fig. 4.19). A second peak in abscission rate was recorded in August, at the start of the second growth period. Abscission rates peaked at between 1.78 and 2.27 leaves shoot$^{-1}$ week$^{-1}$ during winter. This was higher than the rate of leaf production, so the number of leaves per shoot decreased during the die-back period. Similarly, at

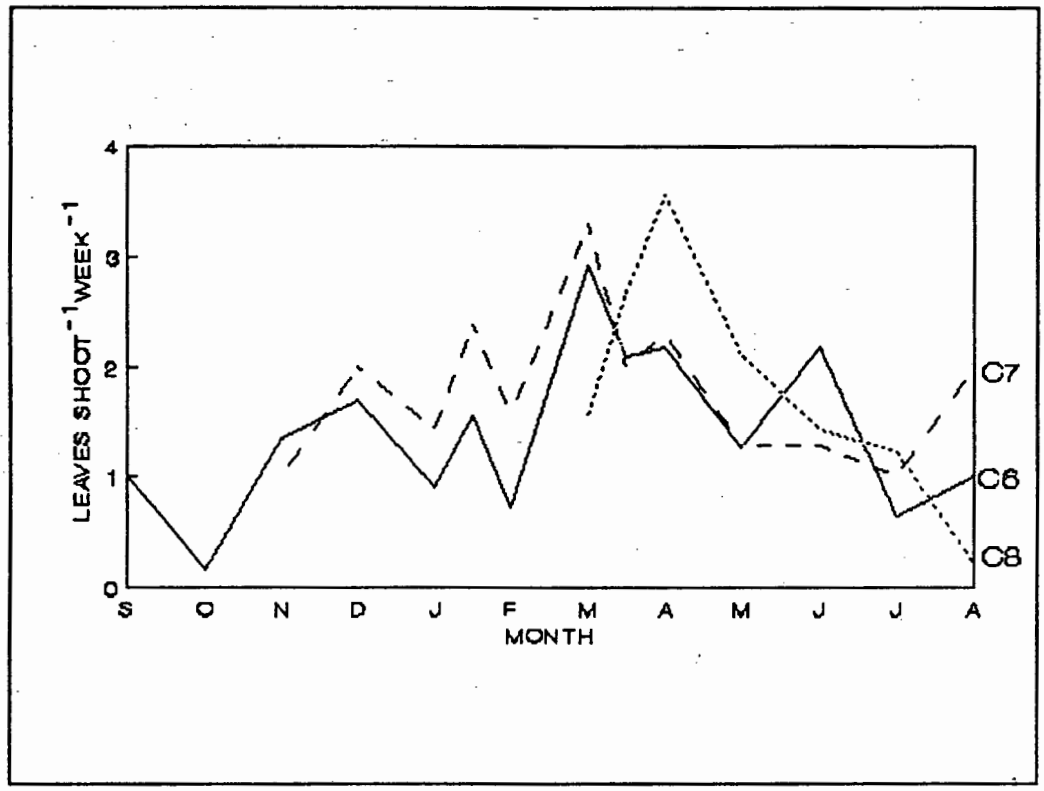



**Figure 4.18:** Variation in leaf death by different cohorts of shoots growing in the seasonally-flooded zone.

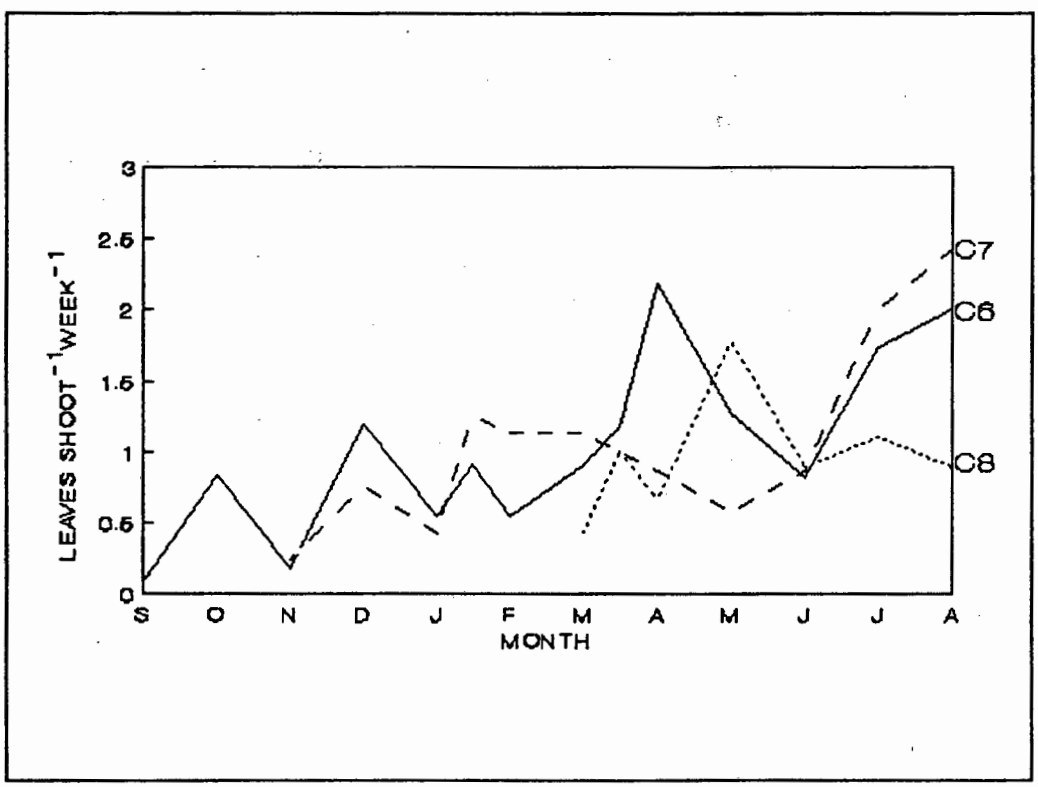



**Figure 4.19:** Variation in leaf abscission rates by different cohorts of shoots growing in the seasonally-flooded zone.

the start of the second growth period, abscission rates exceeded production rates, so the number of leaves per shoot remained low.

## BIOMASS AND PRODUCTION

### Aboveground Shoot Biomass and Standing Crop

The following model was selected to estimate total shoot biomass (more correctly, phytomass) from demographic data, because it provided the best fit to data for all shoot size classes, and for both flowering and for generative shoots:

$$AGB = 0.099(SH) + 0.61(LL) + 1.66(DL)$$
$$(r^2 = 0.94; \quad n = 250),$$

where AGB = AG biomass (or phytomass) (gDW),
SH = shoot height, as length of the longest leaf (cm),
LL = number of live leaves (100% chlorophyllous),
DL = number of dead leaves (0% chlorophyllous).

The use of this model was justified on the grounds that the standing crop calculated from derived shoot biomass estimates were not significantly different to that from harvest data on any occasion (Mann-Whitney U-test, $p<0.05$).

Figure 4.20 illustrates the growth of shoots, as changes in mass, during the study period. During the first season shoot biomass peaked between January and March before decreasing during winter. Mean maximum biomass, which varied between 37.84 and 38.59gDW, was recorded during March 1989. There was no significant difference in the rate of biomass accumulation under different flood regimes.

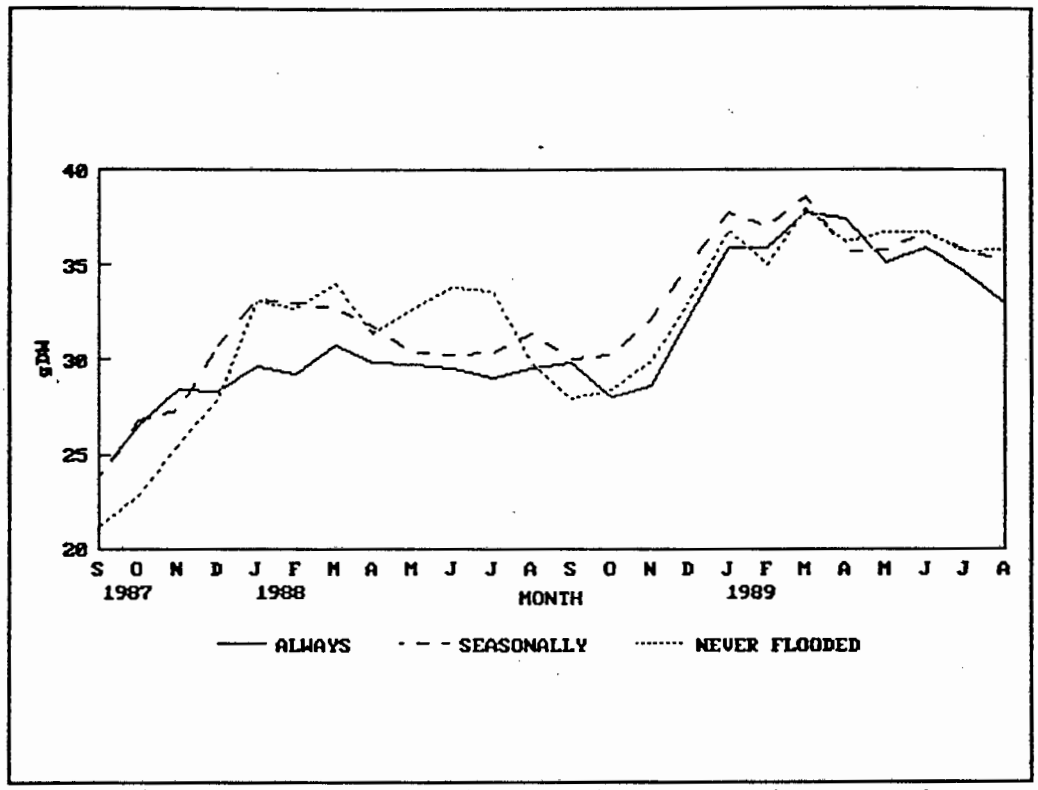



**Figure 4.20:** Seasonal variation in live shoot biomass under different flood regimes.

occasion (van der Valk, 1985). It varied seasonally, following the trends in live shoot density (Fig. 4.21). Standing crop was largest in the seasonally-flooded area where it varied between 887.1 and 1 863.9gDW $m^{-2}$. In the never-flooded area standing crop was higher than that of the always-flooded area during summer, but was similar during winter. Maximum standing crops in these areas were 1 147.3 and 905.5gDW $m^{-2}$ respectively .

The mass of standing litter increased rapidly during winter, especially in the never-flooded area where 585.3gDW $m^{-2}$ was recorded during August 1988 (Fig. 4.22). This was considerably more than that found in the always- (244.8gDW $m^{-2}$) or seasonally-flooded areas (452.9gDW $m^{-2}$). In the wetter areas, standing litter comprised a small proportion of the shoot biomass for most of the season, only becoming dominant when first season shoots began to senesce. The reverse was true for the dry zone: standing litter remained a significant part of the standing biomass until mid-summer when it fell to less than 50gDW $m^{-2}$.

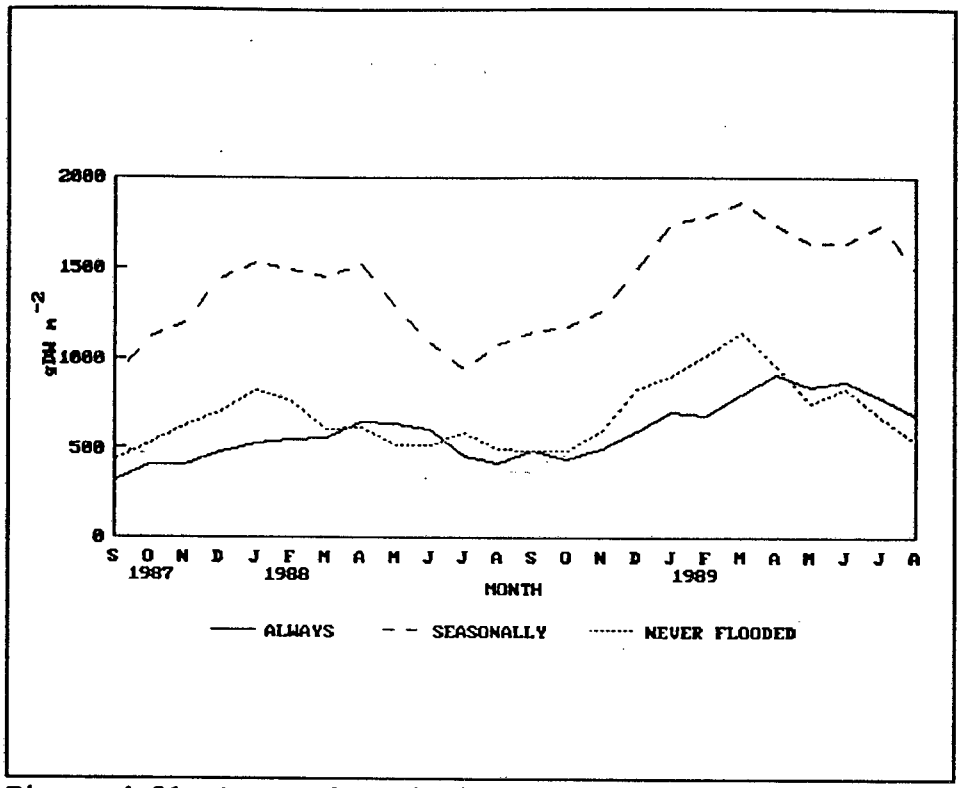



**Figure 4.21:** Seasonal variation in live standing crop under different flood regimes.

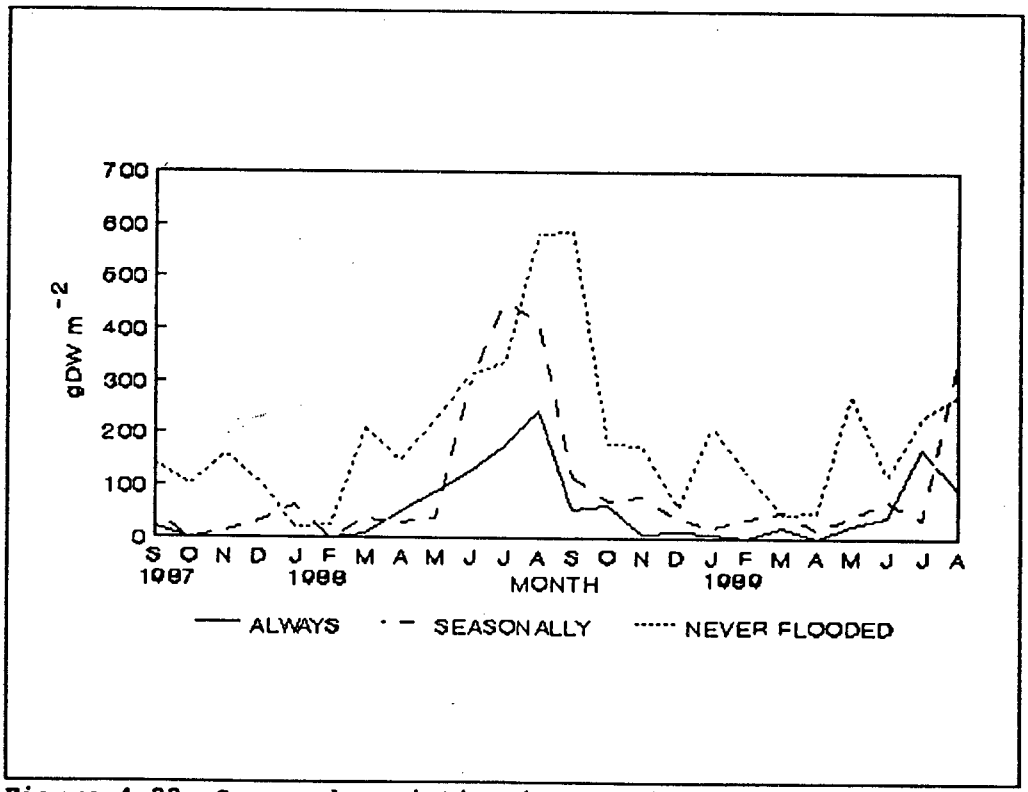



**Figure 4.22:** Seasonal variation in standing litter biomass

The contribution of standing litter to the total standing crop of the dry rushbed can be illustrated by comparing the ratio of standing litter to live shoot biomass under the different flood regimes (Fig. 4.23). While the ratio was only significant during winter (July - August) in the wet zones, it was consistently higher in the dry zone. These differences can be ascribed to differences in litter fall, which is related to shoot base decomposition (Chapter 5).

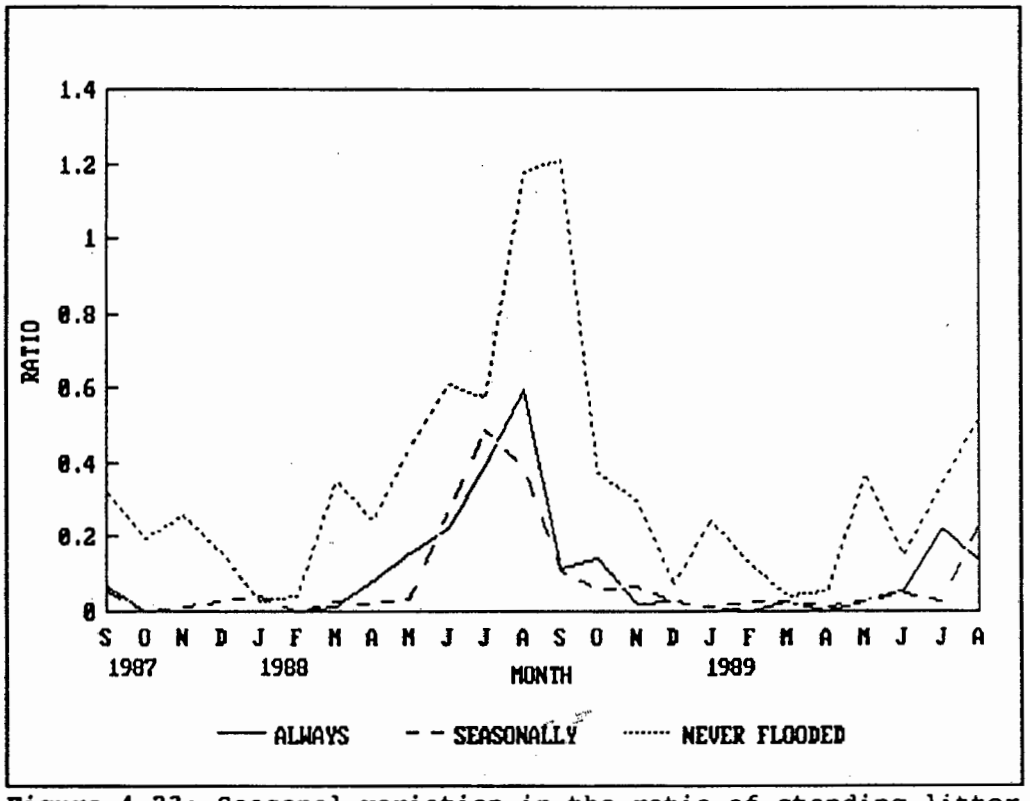



**Figure 4.23:** Seasonal variation in the ratio of standing litter biomass to live standing crop growing under different flood regimes.

**Belowground Biomass**

The BG:AG biomass ratio varied seasonally, with a summer minimum of 1.2:1 and a winter maximum of 26.0:1 (Fig. 4.24). There was a significant increase in rhizome standing crop during late summer, which peaked during the second year at 41.7kgDW $m^{-2}$ in the seasonally-flooded area (Fig. 4.25). This was approximately three months after maximum shoot standing crop had been recorded. In general, rhizome standing crop fell during early summer as reserves

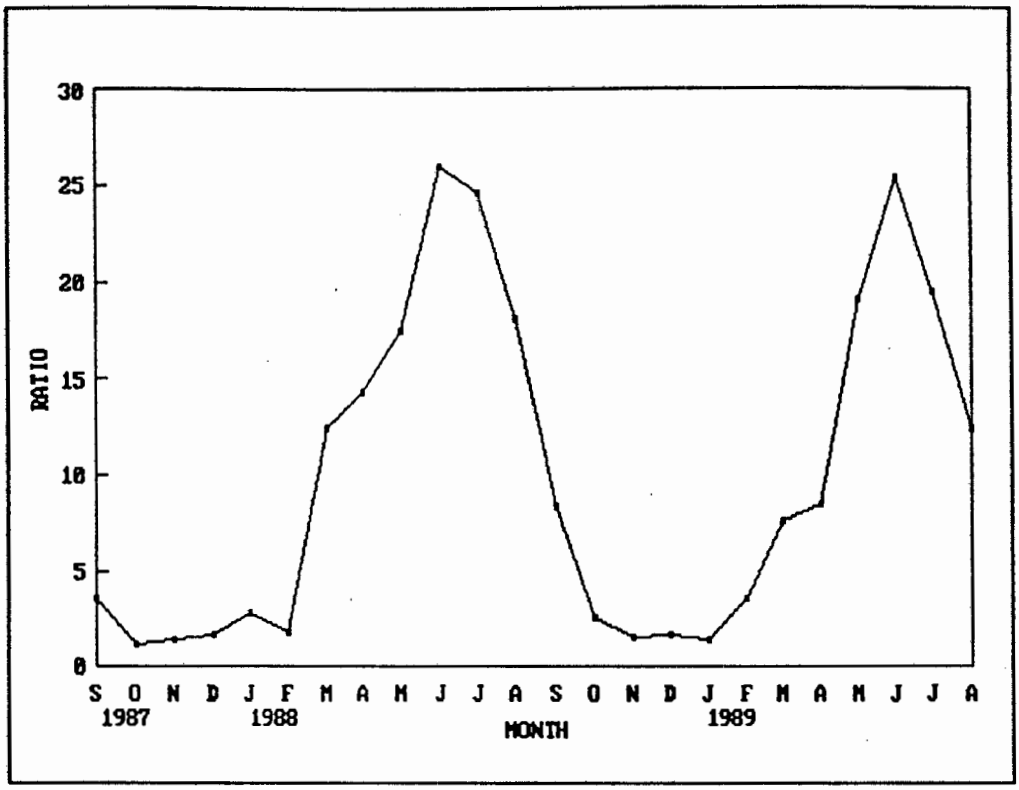



**Figure 4.24:** Seasonal variation in the ratio of belowground biomass to aboveground biomass

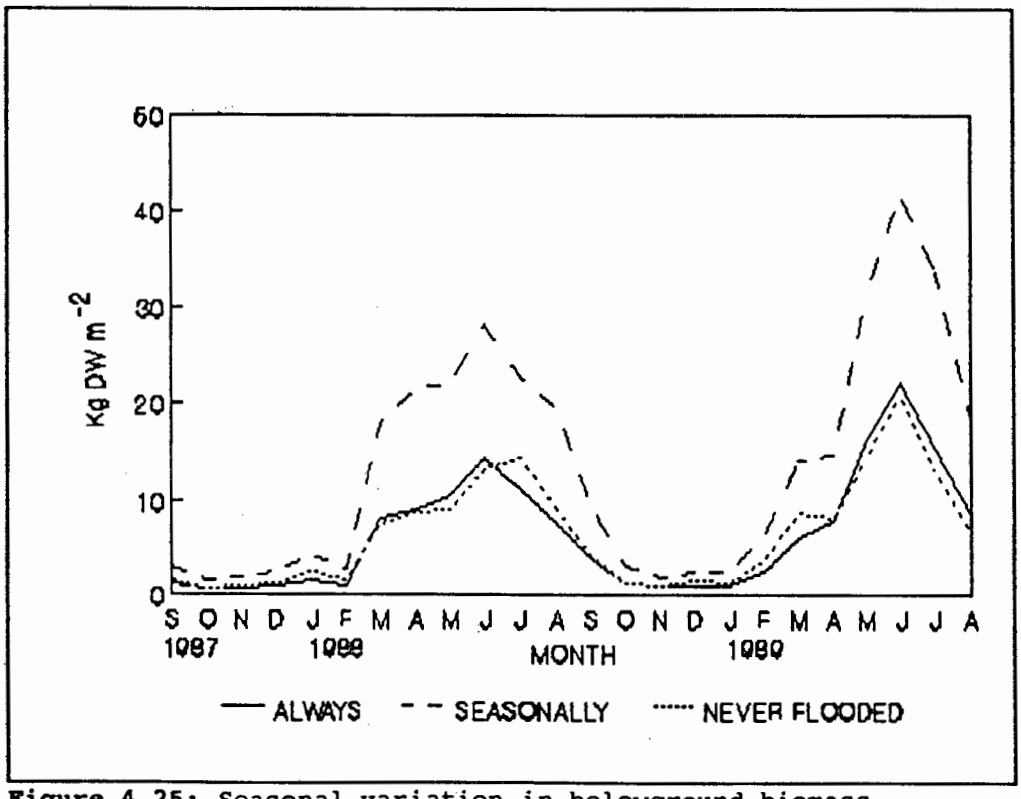



**Figure 4.25:** Seasonal variation in belowground biomass.

were used to fuel emergence. Biomass rose again as shoots began to senesce.

**Biomass-Density Relationships**

The stages of shoot growth are illustrated in figure 4.26. Mean shoot weight increased with no associated shoot mortality until maximum shoot size had been reached. Shoot size then remained relatively constant while shoot density decreased as some shoots died. Finally, biomass decreased as shoots senesced.

The pattern was repeated during the second season, but growth was initiated from the previous season's accumulated biomass. Second-year values are, thus, approximately double those measured of the first year. The biomass density relationship of *Typha* followed the model described by Hutchings & Barkham (1976) (Class A according to Hutchings, 1979). This relationship appeared to hold under all flood regimes, and during both years, despite differences in shoot density.

**Net Production**

Net annual aboveground production (NAAP), net annual belowground production (NABP) and net annual production (NAP) were highest in the seasonally-flooded area, but lowest in the always-flooded area (Table 4.2). This reflects the relative shoot density of the different growth phases.

**TABLE 4.2:** Production by *Typha* growing under different flood regimes in two growth seasons. NAAP - net annual AG production; NABP - net annual BG production; NAP - net annual primary production. Production values in gDW $m^{-2}$.

| REGIME | ALWAYS FLOODED | | SEASONALLY FLOODED | | NEVER FLOODED | |
|---|---|---|---|---|---|---|
| SEASON | 87/88 | 88/89 | 87/88 | 88/89 | 87/88 | 88/89 |
| NAAP | 910 | 560 | 1 635 | 1 432 | 845 | 834 |
| NABP | 1 407 | 2 141 | 2 695 | 3 978 | 1 376 | 2 012 |
| NAP | 1 968 | 2 575 | 3 650 | 4 408 | 1 875 | 2 341 |

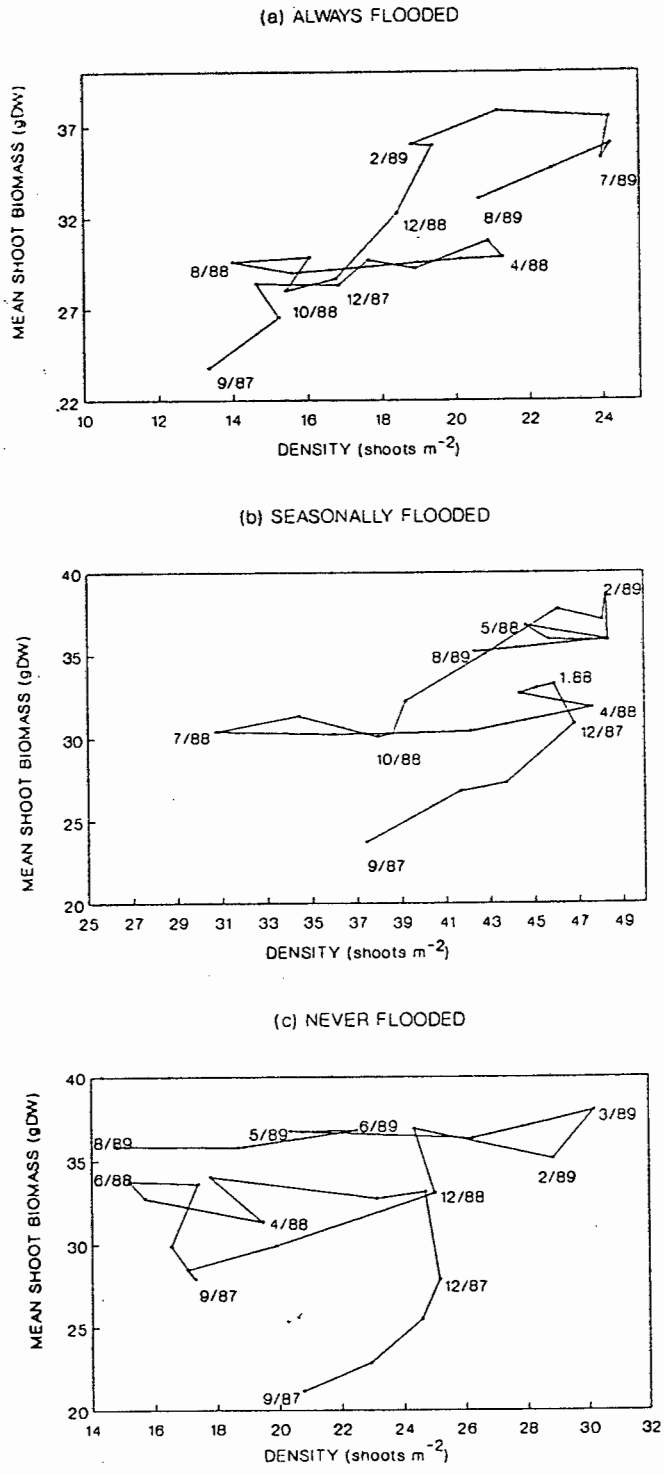



**Figure 4.26:** The relationship between shoot biomass and shoot density in *Typha* stands growing in different flood regimes.

During the first year NAP ranged between 1 875 and 3 650gDW $m^{-2}$, lower than the 2 341 to 4 408gDW $m^{-2}$ recorded during the second year. The annual differences were due to changes in NABP which was higher during the second year while NAP remained within the same range.

Below-ground production was between 0.4 and 2.8 times greater then NAAP, varying between 1 376 and 3 978gDW $m^{-2}$. It was similar in the always- and never-flooded areas, but higher in the seasonally- flooded area. Aboveground production was also highest in the seasonally-flooded zone, where it was between 2 and 3 times as high as in the never- and always-flooded areas.

## DISCUSSION

### PHENOLOGY, DEMOGRAPHY AND LIFE-HISTORY

The absence of seedlings in always-flooded areas and in established *Typha* stands supports reports that seeds do not germinate under water (Beule, 1979), and that seedlings are excluded by mature *Typha* plants (Bonnewell *et al.*, 1983). This has been attributed to the effect of shoots on the intensity and quality of light entering a stand and on associated soil temperature; possible autotoxic and allopathic inhibition has also been reported (Bonnewell *et al.*, 1983; Grace, 1983). Seedling absence in mature stands supports the hypothesis that seedlings do not contribute to the maintenance of stands once they are established (McNaughton, 1968; Grace, 1987).

Seedling mortality was related to drawdown and also to seedling age at drawdown. The primary effect of drawdown was the reduction in water supply, but changes in soil moisture have also been found to affect soil chemistry, primarily increasing salinity (Smith & Kadlec, 1983). Limited water supply and increased soil salinity were probably the major factors causing seedling death in the rushbed studies,

as was the case in studies by Bedish (1967) and Beare & Jedler (1987). The probability of surviving drawdown increased with seedling age because seeds and seedlings are more sensitive to poor conditions than are adult plants (Beare & Jedler, 1987).

The developmental pattern observed in *T. capensis* was similar to that reported for other *Typha* species in so far as shoot growth was interrupted during the winter months, and in that shoot development was only completed during the second growth period (Dickerman, 1982; Gopal & Sharma, 1984; Hultgren, 1988). Unlike most temperate regions, however, growth was only interrupted for a short period; vegetative shoots did not die back completely during winter and most shoots lived for longer than 24 months. This is likely to be a reflection of the Cape's mild winters.

The proportion of fertile shoots in the Rondevlei *Typha* stands was similar to that recorded in other species by Jordan *et al* (1990) and Roberts (1987), but lower than that reported by White & Sinclair (1979; 50%) and Shay & Shay (1986; 22 -68%). Low flowering frequencies appear to be typical of *Typha* stands growing in eutrophic areas, and in closed stands (Grace & Wetzel, 1981b; Jordan *et al.*, 1990). In such stands, where growth is not stressed by nutrient supply, energy is allocated to ramet growth and to vegetative reproduction before the excess is channelled into sexual reproduction (Dickerman & Wetzel, 1985). This suggests that the Rondevlei population may not be producing energy in excess of the vegetative requirements of the stand. As productivity rates were high, this implies that the maintenance and spread of the stand by vegetative reproduction was given priority during energy allocation.

The differences in cohort size between flood regimes recorded in this study has also been noted elsewhere (Waters & Shay, 1991). It seems that the rhizomes

stores of shoots emerging through deep water are depleted before the shoots emerge above the water surface. Submerged immature shoots, unable to meet their own energy requirements, die. In shallower areas, the same energy reserves are sufficient to support growth until the shoot emerged above the water surface and was able to photosynthesise.

High rates of mortality during winter are typical of *Typha* species (Grace & Wetzel, 1981b, Djebrouni & Huon, 1988) and are generally attributed to low temperatures and wind damage. The timing of peak mortality with the conclusion of the growing season indicates an "efficient" growth pattern (Dickerman, 1982).

**SHOOT DYNAMICS**

In this study local temperature differences probably account for some of the differences in growth rates observed between shoots under different flood regimes, but the withdrawal of water supply at drawdown also appears to be important. The effect of drawdown, illustrated by the growth of shoots from C6 and C7 of the never-flooded zone, could be responsible for the differences in growth periods amongst shoots of similar ages, under the different flood regimes. The never-flooded shoots became water limited soon after the onset of drawdown, but those in the wet areas did not, so growth could continue. The relatively long growth periods of seasonally-flooded shoots from C7 and C8 as well as those in the always-flooded zone support this hypothesis.

The densities of shoots in Rondevlei, particularly in the seasoally-flooded area, were similar to those reported elsewhere (Table 4.3). Higher densities have, however, been reported from eutrophic wetlands and from fishponds (Mason & Bryant, 1975; Jordan & Whigham, 1988; van der Valk, 1985). Under both these conditions, and at lower densities (14 shoots $m^{-2}$),

**TABLE 4.3:** Shoot densities of *Typha* species reported in the literature worldwide.

| DENSITY shoots $m^{-2}$ | REFERENCE |
|---|---|
| 12.1 - 48.3 | This study |
| 11.6 - 33.4 | Roberts & Ganf, 1986 |
| 11.2 - 41.9 | Dickerman, 1982 |
| 12.7 - 43.9 | Dickerman, 1982 |
| 13.3 | Djebrouni & Huon, 1988 |
| 14.3 | Ogden, 1981 |
| 14 - 38 | Bernard & Fitz, 1979 |
| 15 - 25 | Kvet *et al.*, 1969 |
| 17 | Klopatek & Stearns, 1978 |
| 17 - 41 | Fiala, 1971 |
| 21 - 32 | Boyd, 1971 |
| 25.6 - 38.8 | Lieffers, 1983 |
| 26 - 40 | Shay & Shay, 1986 |
| 30 - 120 | Grace, 1989 |
| 30 | White & Sinclair, 1979 |
| 33 - 79 | Jordan *et al.*, 1990 |
| 34 | Hogg & Wein, 1987 |
| 36.3 - 93.3 | Penko & Pratt, 1985/86 |
| 37 - 40 | Dickerman & Wetzel, 1985 |
| 41 | Beule, 1979 |
| 40 - 50 | Krusi & Wein, 1988 |
| 45 - 68 | van der Valk & Davis, 1980 |
| 45 - 79 | van der Valk, 1985 |
| 60 | Grace, 1988 |
| 84 | Jordan & Whigham, 1988 |
| 100 | Mason & Bryant, 1975 |
| 108 | Dykyjova, 1978 |

self-thinning has been observed (Mason & Bryant, 1975; Ogden, 1981). It is, therefore, possible that the Rondevlei population was subject to density-mediated stresses. Symptoms of such stresses include high juvenile mortality and high rates of generative shoot mortality during the growing season (Bradbury, 1981). While such symptoms were recorded in the never-flooded zone, they were absent in the seasonally- and always-flooded areas. As shoot densities in the seasonally-flooded area were considerably higher than those in the never-flooded area, it is unlikely that increased rate of mortality was density mediated; it is more likely that summer mortality was due to moisture-limitation (e.g. Roberts, 1987).

The way in which shoot density is regulated under different flood regimes has important consequences for both stand production and structure. In cold-temperate areas, where all shoots die during winter so that stands have to become reestablished every year, species which can most quickly produce the largest canopy enjoy a preemptive advantage. This makes annual recruitment and shoot establishment patterns vital to stand success. In Rondevlei, where the stands were never entirely removed, but where winter mortality created gaps in the stands, shoot establishment patterns were important, preventing stand invasion by species able to exploit gaps in the *Typha* canopy. Data on shoot emergence showed marked differences in shoot establishment patterns between stands growing under different flood regimes (Fig. 4.5). This is significant in terms of their productivity, because stand production will be highest in areas where the maximum possible number of shoots are present for the greatest part of the growing season.

The rapid rate of emergence in never-flooded areas should have made these the most productive areas, but the growing period was reduced by drawdown (Figs. 4.5

and 4.10). Instead, rapid recruitment maximised production during the period when water was not limited. The never-flooded area was also the most vulnerable to invasion by terrestrial plants. Invasion is minimised by high rates of emergence in early spring, filling spaces created by winter mortality and shoot collapse.

Spaces created in the seasonally- and always-flooded areas in Rondevlei were filled gradually, with shoot saturation only being reached at the end of summer (Fig. 4.14) In these areas energy reserves were used to increase the rate of successful establishment rather than to produce many shoots with a lower success rate. Such a conservative means of recruitment was suitable for the conditions prevailing in the seasonally-flooded area, where new shoots effectively filled the gaps created by shoot death, but seemed less suitable for the always-flooded area, where shoot density was low and where the stand was unlikely to have been shoot-saturated. Perhaps the relatively high water levels during early spring inhibited recruitment until drawdown.

**BIOMASS AND PRODUCTION**

Mean shoot biomass for Rondevlei (37.84gDW) was generally higher than those reported in the literature (21.75gDW - Mason & Bryant, 1975; 36.7gDW - Dykyjova, 1978; 27.3 - 34.0gDW - Dickerman, 1982; 15.0 to 31.1gDW - Lieffers, 1983). This difference accounts for the fact that the standing crop in Rondevlei rushbeds lies close to the top end of the range reported for other *Typha* species (Table 4.4). It also reflects the longer, warmer growing season experienced in the Cape. The variation between flood regimes was similar to that reported by Djebrouni & Huon (1988) who found that standing crops increased from pond periphery to its centre in response to changes in water depth.

**TABLE 4.4:** Reported values for *Typha* standing crop. AG - aboveground biomass; BG - belowground biomass (gDW $m^{-2}$).

| SPECIES | AG | BG | REFERENCE |
|---|---|---|---|
| *T. capensis* | 905-1864 | | This study |
| | 125-324 | | O'Callaghan, 1980 |
| *T.* X *glauca* | 2000 | 1431 | Davis & v d Valk, 1983 |
| | 166-1360 | | Bernard & Fitz, 1979 |
| | 772-1075 | | v d Valk & Davis, 1980 |
| | 1103-2320 | 2650-3100 | Pratt & Andrews, 1980 |
| *T. latifolia* | 1754 | 2526 | Shay & Shay, 1986 |
| | 781 | 605 | Shay & Shay, 1986 |
| | 3000-5000 | | Grace, 1987 |
| | 1600 | | Beule, 1979 |
| | 756-848 | 383-807 | Lieffers, 1983 |
| | 500-2000 | 200-1400 | Pratt & Andrews, 1980 |
| | 1700 | | Pelikan *et al.*, 1970 |
| *T. domingensis* | | 1350 | Jones, 1988 |
| | 142-1306 | 678-3562 | Roberts & Ganf, 1986 |
| *T. angustifolia* | | 247-564 | Jordan et al., 1990 |
| | 1118 | | Mason & Bryant, 1975 |
| | 1843-3216 | 309-569 | Hill, 1987 |
| | 100-3000 | 900-3600 | Pratt & Andrews, 1980 |
| | >1000 | | Ksenofontova, 1989 |
| *Typha* spp. | 1700 | | Pelikan *et al.*, 1970 |
| | 455 | 1500 | Hogg & Wein, 1987 |
| | 1600 | | Beule, 1979 |

When growth is restricted by abiotic factors, the relationship between standing crop and density becomes uncoupled at high densities. Further growth is then dependent on the rate of supply of the limiting resource (Kira *et al.*, 1953; Shinozaki & Kira, 1956). In Rondevlei, AG biomass was clearly dependent on shoot density over all observed densities, indicating that external resources were not limiting production. The close relationship between shoot density and standing crop also suggests that density, rather than individual shoot mass, determined AG biomass, thus supporting reports by Klopatek & Stearns (1978), Boyd & Hess (1970) and Dickerman (1982). In other plants, aerial production increases at low shoot densities so that biomass production remains constant despite density differences (White & Sinclair, 1979).

Standing litter densities in Rondevlei were generally much lower than those reported in *Typha* stands from Canada and Australia (Table 4.5). This is an unexpected result in light of the high live standing crop recorded in the vlei (Fig. 4.21), and it may indicate that standing litter collapse and decomposition rates are higher than the average recorded in other marshes (see Chapter 5).

**TABLE 4.5:** Reported values for *Typha* litter standing crop.

| SITE | SPECIES | STANDING LITTER gDW $m^{-2}$ | REFERENCE |
|---|---|---|---|
| S.Africa | *T. capensis* | 245-585 | This study |
| Canada | *T. latifolia* | 1224 | Shay & Shay, 1986 |
| Canada | | 715 | Shay & Shay, 1986 |
| Australia | *T. domingensis* | 902-2509 | Roberts & Ganf,1986 |

The changing ratio of BG:AG biomass recorded in Rondevlei is similar to those reported for *Typha* from Australia (Roberts, 1987) and North America (Ulrich & Burton, 1985, 1988; Hill, 1987), but considerably higher than reports from Europe (Merezhko *et al.*, 1979; Sharma & Pradhan, 1983; Hogg & Wein, 1987).

However, this ratio does vary both seasonally (Roberts, 1987) and with nutrient supply (Reddy & DeBusk, 1987), making direct comparisons difficult. Nevertheless, the higher ratio for Rondevlei indicates that rhizome stores were larger than those areas with a lower BG:AG ratio. This may be due to the relatively mild climate of the Cape Flats (this study), Texas (Hill, 1987) and Australia (Roberts, 1987) where, because production continues all year, rhizome stores are never depleted, thereby allowing higher rates of BG biomass accumulation.

The accumulation of rhizome biomass by *Typha* late in the growing season, as was noted in Rondevlei, has been shown to be associated in other studies with an increase in rhizome nutrient and starch levels (e.g. Linde *et al.*, 1976). It is generally held that the nutrients are withdrawn from the shoots themselves while the increase in rhizome energy level is due to the storage of photosynthate as non-structural carbohydrates in the rhizomes (Linde *et al.*, 1976; Gopal & Sharma, 1984; Smith *et al.*, 1988). On the other hand, BG standing crop was relatively high by comparison to similar studies elsewhere (Table 4.4), probably reflecting the mild climate of the Cape, under which growth did not stop during winter. Such continuous growth reduced the drain on rhizome reserves.

The ten-fold range in estimates of production by *Typha* reported in the literature (Table 4.6), can be attributed to production varying with species and between sites as climate, nutrient and water supply differ (Mason & Bryant, 1975; Dykyjova, 1978; Adriano *et al.*, 1980). The production estimates for Rondevlei lie at the top end of this range (Table 4.6). This may be because most of the reported values were derived from areas where production was halted during winter.

The effect of flood regime on production at Rondevlei

**TABLE 4.6:** Reported estimates of *Typha* production. NAAP - net annual AG production; NABP - net annual BG production; NAP - net annual production, all in gDW $m^{-2}$.

| SPECIES | NAAP | NABP | NAP | REFERENCE |
|---|---|---|---|---|
| *T. capensis* | 560-1635 | 1376-3978 | | 1875-4408 This study |
| | 1249 | | | Howard-Williams, 1980 |
| *T.* X *glauca* | 1281 | | | vd Valk & Davis, 1978 |
| | 1130 | 3100 | 4230 | Pratt & Andrews, 1980 |
| | 1156 | | | Davis & vd Valk, 1983 |
| | 790-1100 | | | van der Valk, 1985 |
| | 1476 | | | Bernard & Fitz, 1979 |
| | 346-926 | | | Penko & Pratt, 85/86 |
| *T. orientalis* | 1187 | 2884 | 4071 | Roberts & Ganf, 1986 |
| *T. latifolia* | 330-418 | | 1160 | McNaughton, 1966 |
| | 730 | 804 | 1534 | McNaughton, 1966 |
| | 686 | | | Boyd & Hess, 1970 |
| | 530-1132 | | | Boyd, 1971 |
| | 456-848 | | | Lieffers, 1983 |
| *T.angustifolia* | 1445 | | | Mason & Bryant, 1975 |
| | 330-1905 | 371-1868 | | Hill, 1987 |
| | 807 | 3996 | | Anderson, 1976 |
| *T. elephantina* | 975-2464 | | | Sharma & Gopal, 1977 |
| *Typha* spp. | 404 | 912 | 1316 | McNaughton, 1966 |
| | 1122-2537 | | | Kalk *et al.*, 1979 |
| | 1623-2173 | 1679 | | Neeley & Davis, 1985 |
| | 455 | | 249 | Hogg & Wein, 1987 |

was marked, with always- and never-flooded shoots being less productive than those which were seasonally-flooded. In the seasonally-flooded area NAP was approximately 45% greater than that recorded in the other parts of the same rushbed. The relatively low NAP recorded in never- and always-flooded areas reflects the different negative aspects of their immediate environments. Water supply probably limited productivity in the never-flooded area (Fiala & Kvet, 1971; van der Valk, 1985) while the low production rate recorded amongst always-flooded shoots was a reflection of low shoot density.

**STAND STRUCTURE**

Plant zones, or growth phases, are usually visible where clonal species have become established. For example, *Carex arenaria* forms zones around the base of the mobile dunes with which it is associated (Noble *et al.*, 1979). As the *Carex* colony develops, its appearance changes because early growth phases are replaced by later phases; an area initially colonised by the juvenile phase is eventually characterised by the adolescent phase, while the adolescent phase is followed by a mature phase. Once the colony enters the mature phase it begins to colonise surrounding areas and it creates satellite stands in the juvenile phase. The change from one phase to another represents a continuum (Noble *et al*, 1979). Three such growth phases were identified within the *Typha* stand colonising the littoral zone of Rondevlei, corresponding to the juvenile, mature and senile phases described above. The position of the growth phases was clearly related to flooded regime, being associated with areas which were always-, seasonally- and never-flooded respectively.

The growth phases for Rondevlei were defined according to their demographic structure. The senile phase, limited to areas which were never-flooded, was characterised by high generative shoot density, low juvenile shoot density and a large standing litter crop. Shoot biomass was reduced in a way similar to that of shoots growing in areas which had been drained (i.e. reduced shoot height, shorter growing period, lower shoot density and increased litter accumulation) (Krusi & Wein, 1988). By shading the sediments, litter limits the emergence of new shoots (see also Chapter 6). Drought shortened the length of the growing period of shoots emerging in late summer, but this did not limit production because these shoots had a higher growth rate (Fig. 4.9). This may be attributed to the warming of the unflooded sediments. The net result was a phase dominated by standing

litter and by generative live shoots, the productivity of which was limited by water supply in summer. Live standing crop and production in this area were consequently low (Fig. 4.20, Table 4.2). In both years, shoot mortality exceeded emergence (Figs. 4.4 and 4.5) indicating that live shoot density was declining.

At the other end of the flood regime, in the always-flooded zone, the juvenile growth phase appeared. Here shoot density was low (Fig. 4.13) and the zone was characterised by approximately equal numbers of generative and juvenile shoots (Fig. 4.10). Standing crop and production rates were relatively low (Fig. 4.20, Table.4.2). This was mainly due to the low rate of shoot emergence (Fig. 4.4). The growth rate of new shoots was lower than that recorded in other phases (Fig. 4.9), but maximum shoot size was not statistically significantly different (Fig. 4.17) because of the longer growing period. Annual mortality rate was double the recruitment rate, thus indicating that the rushes were not successfully colonising this area.

Production in the mature growth phase was high, a reflection of high generative shoot density (Fig. 4.13) and the long growth period observed in the seasonally-flooded area (Fig. 4.9). This zone was dominated by generative shoots, but standing litter and juvenile shoots were also present in small proportions (Fig. 4.11). During the first season, shoot emergence exceeded mortality, with a corresponding increase in density and production (Fig. 4.13, Table 4.2). During the second year, however, mortality was higher than recruitment (Figs. 4.4 and 4.5). This may indicate that the area had reached its carrying capacity, and that shoot densities could not exceed those recorded during 1987/1988 without incurring density stress.

These growth phases represent the different

developmental stages in the formation of a *Typha* stand. As a stand becomes established it invades neighbouring areas until it reaches an area unsuitable for growth. In the rushbed described here the mature growth phase represents the actively colonising part of that stand. Production was able to continue throughout the year as the area had an adequate water supply during summer, but was not subjected to high water levels during the wet winter months. Under such conditions, abiotic factors appear to favour stand encroachment, and production is limited only by biotic factors such as density-mediated stress.

The always-flooded area represents the inhospitable environment into which the stand is forced if it is to continue to expand. As *Typha* is generally restricted to areas where water depth is <1.0m (Grace & Wetzel, 1981b), it seems likely that the increase in water depth (to 1.2m) during winter inhibits colony spread. This hypothesis is supported by evidence that there was no shoot emergence once the wetland had been reflooded, and that winter mortality in this area was higher than in the seasonally-flooded zone. The growth phase was maintained by summer growth. Shoots emerging in the warm, damp margins created by drawdown appear to be invading the area, but subsequent winter flooding increased mortality, preventing successful stand establishment.

Expansion towards the landward wetland margins was inhibited by the high density of shoots and standing litter in the senile growth phase. These shoots effectively blocked invasion in two ways: firstly, the canopy shaded the area, preventing the emergence or germination of new shoots, and secondly, BG biomass physically filled the sediments and prevented the expansion of rhizomes from surrounding generative shoots into the senile zone (e.g. Eleuterius, 1976). Rhizomes continue to fill the sediments long after the area has entered the senile phase. Hogg & Wein (1987) have shown that they can live in excess of six years,

while Hill (1985) has shown that rhizomes decompose slowly under anoxic conditions. These inhibitory conditions are typical of the senile growth phase of clonal plants (Noble *et al.*, 1979).

The relationship between the growth phases and flood regime is significant as changes from one phase to another appear to be related to hydrosere succession. The senile phase is the remnant of a previously mature phase, which has been replaced as drier conditions reduce the competitive edge *Typha* has over terrestrial species. The mature phase dominates the seasonally-flooded zone, and invades the always-flooded areas. As hydrosere succession continues, relative water depth in the always-flooded area falls until flooding no longer inhibits production. Once the source of stress e.g. deep water, is removed, the stand moves into the formerly always-flooded area with the mature phase replacing the juvenile one.

The encroachment process is self-perpetuating and "terrestrialisation" is caused by the build-up of organic and inorganic material. In rushbeds this is enhanced by the high rate of production which contributes plant material to the sediment layer (Godshalk & Barko, 1985). The shoots also reduce circulation and form a sieve which traps silt and other material. Thus, as shoot density and production increase, so does siltation and the colonised area becomes increasingly dry and unsuitable for *Typha* growth.

**COMPARISON OF STAND AND SHOOT DEMOGRAPHY AS REVEALED BY ANALYSIS OF SHOOT AND LEAF DEMOGRAPHY**

The recruitment of new leaves peaked in October, one month after the peak in shoot emergence (Figs. 4.15 and 4.4). This lag suggests that shoot growth begins to accelerate approximately 30 days after the shoot first appears.

Recruitment of both new leaves (Fig. 4.15) and shoots (Fig. 4.4) was low during the period of drawdown, emphasising the negative effect of drought on *Typha* growth. Despite moisture limitation, new shoots were produced during summer, and these shoots produced new leaves at rates similar to those recorded for C6 and C7 shoots after their emergence (Fig. 4.15). The physiological dependence of newly emerged shoots on their parent ramet may be important in this regard. Both the energy and moisture requirements for emergence and growth can be provided by the parent ramet, upon which the daughter shoot is physiologically dependent (Hartnett & Bazzaz, 1983; Salzman & Parker, 1985; Roberts, 1987; Jordan & Whigham, 1988).

The trends in senescence were similar both for leaves and shoots with leaf senescence peaking approximately one month prior to shoot senescence (Figs. 4.16 and 4.3) and reflecting the lag between leaf and shoot response to environmental cues. A similar lag in peak mortality rate, associated with either drought stress or winter die-back, was recorded. This trend was not mirrored by leaf abscission/shoot collapse rates (Fig. 4.18 and 4.3). Leaf abscission followed approximately one month after leaf death (Figs. 4.18 and 4.19), but shoot collapse in the never-flooded area (Chapter 5) was generally confined to the period between July and September. Thus, standing litter remains part of the shoot much longer than necromass.

A comparison of the results of demographic trends revealed by examining both shoots and leaves indicates that similar patterns of recruitment and mortality are apparent no matter what plant module is studied. Precise timing of events may vary as, for example, leaf recruitment followed shoot emergence, or leaf death preceded shoot death. On the other hand, life-history characteristics revealed by examining their demographic development were less similar. For example, leaf production continued throughout the

year, showing that growth does not stop either during winter flooding or during the summer drought period. However, shoot demography revealed that emergence between January and June was virtually nil, suggesting that growth was suspended during the drought period. The difference is essentially one of scale, with shoot demography revealing gross changes, and leaf demography reflecting less obvious ones.

## CONCLUSIONS

1. Three growth phases, juvenile, mature and senile, were identified within the *Typha* stand of Rondevlei. They were restricted to areas within the littoral zone that were respectively always-, seasonally- or never-flooded. Stand structure was thus closely related to flood regime, but probably changed as hydrosere succession proceeded.

2. Recruitment within the stand was by vegetative rather then by sexual reproduction. Seedlings were confined to cleared areas not covered by water, suggesting that they play an invasive, rather than a maintenance role in *Typha* life-history.

3. Production was highest in the area which was seasonally-flooded. It was enhanced by a high rate of recruitment (by seedlings and vegetative shoots), by low juvenile mortality, by longevity among vegetative shoots and by high shoot density.

4. Shoot growth was highest in areas that were never-flooded, but production in this area was limited by the relatively low density of generative shoots, and by their short growing season. Growth was curtailed by drawdown,

which also limited recruitment by interfering with shoot emergence.

5. Production was lowest in the always-flooded area, where shoot densities and growth rates were low. Deep water during winter floods appeared to restrict the colonisation of this area. It also increased mortality amongst one- and two-year old shoots.

6. *T. capensis* was most successful in areas where soil moisture remained high, but where the shoots were never flooded by water deeper than half a metre. Deeper water, or drier conditions, reduced stand productivity.

7. Changes in ramet and leaf structure revealed similar demographic trends, suggesting that either ramet or leaf can be used to study the demographic development of clonal species. Leaves, however, were more sensitive as indicators of life-history changes, and are recommended for studies which require information on a finer scale.

## REFERENCES

ADRIANO, D.C., FULENWIDER, A., SHARITZ, R.R., CIRACALO, T.G. & HOYT, G. 1980. Growth and mineral nutrition of cattail *Typha latifolia* as influenced by thermal alteration. *J. Environ. Qual.*, 9: 649-453.

ANDERSON, F.O. 1976. Primary production in a shallow water lake with special reference to a reed swamp. *Oikos*, 27: 243-250.

BAZZAZ, F.A. & HARPER, J.L. 1977. Demographic analysis of the growth of *Linum usitattissimum*. *New Phytol.*, 78: 193-208.

BEARE, P.A. & JEDLER, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh - the role of salinity intrusion. *Estuaries*, 10: 165-170.

BEDISH, J.W. 1967. Cattail moisture requirements and their significance to marsh management. *Am. Midl. Nat.*, 78: 288-300.

BERNARD, J.M. 1975. The life-history of shoots of *Carex lacustris*. *Can. J. Bot.*, 53: 256-260.

BERNARD, J.M. & MACDONALD, J.G.Jr. 1974. Primary production and life-history of *Carex lacustris*. *Can. J. Bot.*, 52: 117-123.

BERNARD, J.M. & SOLSKY, B.A. 1977. Nutrient cycling in a *Carex lacustris* wetland. *Can. J. Bot.*, **55**: 630-638.

BERNARD, J.M. & GORHAM, E. 1978. Life-history aspects of primary production in sedge wetlands. In: *Freshwater Wetlands. Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York, London.

BERNARD, J.M. & FITZ, M.L. 1979. Seasonal changes in above-ground primary production and nutrient contents in a central New York *Typha glauca* ecosystem. *Bull. Torrey Bot. Club*, **106**: 37-40.

BEULE, J.D. 1979. *Control and management of cattails in south-eastern Wisconsin wetlands*. Tech. Bull. No. 112, Dept. Nat. Res., Madison, Wisconsin.

BONNEWELL, V., KOUKKARI, W.L. & PRATT, D.C. 1983. Light, oxygen and temperature requirements for *Typha latifolia* seed germination. *Can. J. Bot.*, **61**: 1330-1336.

BOYD, C.E. 1971. Further studies on the productivity, nutrient and pigment relationships of *Typha latifolia* populations. *Bull. Torrey Bot. Club*, **98**: 144-150.

BOYD, C.E. & HESS, L.W. 1970. Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. *Ecology*, **51**: 296-300.

BRADBURY, I.K. 1981. Dynamics, structure and performance of shoot populations of the rhizomatous herb *Solidago canadensis*. *Oecol.*, **48**: 271-276.

BRUX, H., TODESKINO, D. & WIEGLEB, G. 1987. Growth and reproduction of *Potamogeton alpinus* Balbis growing in disturbed habitats. *Arch. Hydrobiol.*, **27**: 115-127.

DAVIS, C.B. & VAN DER VALK, A.G. 1983. Uptake and release of nutrients by living and decomposing *Typha glauca* Godr. tissue at Eagle Lake, Iowa. *Aquat. Bot.*, **16**: 75-89.

DICKERMAN, J.A. 1982. Pattern and process of clonal growth in a common cattail (Typha latifolia L.). DOE/EV/01599-219-Pt4. NTIS Order No. DE82021971;COO-1599-219-Pt4; Contract AC02-76EV01599.

DICKERMAN, J.A., STEWART, A.J. & WETZEL, R.G. 1986. Estimates of annual aboveground production: Sensitivity to sampling frequency. *Ecology*, **67**: 650-659.

DICKERMAN, J.A. & WETZEL, R.G. 1985. Clonal growth in *Typha latifolia*: Population dynamics and demography of the ramets. *J. Ecol.*, 73: 535-552.

DJEBROUNI, M. & HUON, A. 1988. Structure and biomass of a *Typha* stand revealed by multidimensional analysis. *Aquat. Bot.*, **39**: 331-342.

DYKYJOVA, D. 1978. Nutrient uptake by littoral communities of helophytes. In: *Pond Littoral Ecosystems: Structure and function*. Dykyjova, D. & Kvet, J. (eds). Springer-Verlag, Berlin.

ELEUTERIUS, L.N. 1976. Vegetative morphology and anatomy of the salt marsh plant *Juncus roemerianus*. *Gulf Res. Rep.*, **5**: 1-10.

FIALA, K. 1971. Seasonal changes in the growth of clones of *Typha latifolia* L. in natural conditions. *Folia Geobot. Phytotaxon.*, 6: 225-270.

FIALA, K. & KVET, J. 1971. Dynamic balance between plant species in South Moravian reedswamps. In: *The Scientific Management of Animal and Plant Communities for Conservation*. Duffey, E. & Watt, A.S. (eds). 11th Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford.

GARDINER, A.J.C. 1988. *A study on the water chemistry and plankton in blackwater lakelets of the Southwestern Cape*. PhD Thesis, Department of Zoology, University of Cape Town, Cape Town.

GODSHALK, G.L. & BARKO, J.W. 1985. Vegetative succession and decomposition in reservoirs. In: *Microbial Processes in Reservoirs*. Gunnison, D. (ed.). Dr W. Junk Publishers, Dordrecht.

GOPAL, B & SHARMA, K.P. 1984. Seasonal changes in concentration of major elements in the rhizomes and leaves of *Typha elephantina* Roxb. *Aquat. Bot.*, **20**: 65-73.

GRACE, J.B. 1983. Autotoxic inhibition of seed germination by *Typha latifolia*: An evaluation. *Oecol.*, **59**: 366-369.

GRACE, J.B. 1987. The impact of pre-emption on the zonation of two *Typha* species along lake shores. *Ecol. Mono.*, **57**: 283-303.

GRACE, J.B. 1988. The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water-level gradient. *Aquat. Bot.*, **31**: 83-92.

GRACE, J.B. 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *Am. J. Bot.*, **76**: 762-768.

GRACE, J.B. & WETZEL, R.G. 1981a. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia*: Experimental studies in marshes of differing successional maturity. *Ecology*, **62**: 789-801.

GRACE, J.B. & WETZEL, R.G. 1981b. Effect of size and growth rate on vegetative reproduction in *Typha*. *Oecol.*, **50**: 158-161.

GUSTAFSON, T.D. 1976. *Production, Photosynthesis and the Storage and Utilization of reserves in a natural stand of Typha latifolia*. PhD Thesis, University of Wisconsin.

HARPER, J.L. 1985. Modules, branches and the capture of resources. In: *Population Biology and Evolution of Clonal Organisms*. Jackson, J.B.C., Buss, L.W. & Cook, R.E. (eds). Yale University Press, New Haven.

HARTNETT, J.C. & BAZZAZ, F.A. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology*, **64**: 779-788.

HILL, B.H. 1985. The breakdown of macrophytes in a reservoir wetland. *Aquat. Bot.*, **21**: 23-31.

HILL, B.H. 1987. *Typha* production in a Texas pond: Implications for energy and nutrient dynamics in freshwater wetlands. *Aquat. Bot.*, **27**: 385-394.

HOGELAND, A.M. & KILLINGBECK, K.T. 1985. Biomass, productivity and life-history traits of *Juncus militarus* Bigel. in two Rhodes Island (USA) freshwater wetlands. *Aquat. Bot.*, **22**: 335-346.

HOGG, E.H. & WEIN, R.W. 1987. Growth dynamics of floating *Typha* mats: Seasonal translocation and internal deposition of organic material. *Oikos*, **50**: 197-205.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophyte communities of the Wilderness Lakes: Community structure and associated environmental conditions. *J. Limnol. Soc. sth. Afr.*, **6**: 85-92.

HULTGREN, A.B.C. 1988. A demographic study of aerial shoots of *Carex rostrata* in relation to water level. *Aquat. Bot.*, **30**: 81-93.

HUTCHINGS, M. 1979. Weight-density relationships in a ramet population of clonal perennial herbs, with special reference to the -3/2 power law. *J. Ecol.*, **67**: 21-23.

HUTCHINGS, M.J. & BARKHAM, J.P. 1976. An investigation of shoot interactions in *Mercurialis perennis* L., a rhizomatous perennial herb. *J. Ecol.*, **64**: 723-743.

JEFFERIES, R.L. 1984. The phenotype: Its development, physiological constraints and environmental signals. In: *Perspectives in Plant Ecology*. Dirzo, R. & Sarakhan, J. (eds). Sinauer Associates, Sunderland.

JONES, M.B. 1988. Photosynthetic responses of C3 and C4 wetland species in a tropical swamp. *J. Ecol.*, **76**: 253-262.

JORDAN, T.E. & WHIGHAM, D.F. 1988. The importance of standing dead shoots of the narrow leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **29**: 319-328.

JORDAN, T.E., WHIGHAM, D.F. & CORRELL, D.L. 1990. Effects of nutrient and litter manipulations on the narrow leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **36**: 179-191.

KALK, M.J., MCLACHLAN, A.J. & HOWARD-WILLIAMS, C. (eds). 1979. *Lake Chilwa: Studies of change in a tropical ecosystem*. Dr W. Junk Publishers, The Hague.

KIRA, T., OGAWA, H. & SHINOZAKI, K. 1953. Intra-specific competition among higher plants. 1. Competition-density yield inter-relationships in regularly dispersed populations. *J. Inst. Polytech., Osaka City Univ. D.*, **4**: 1-16.

KLOPATEK, J.M. & STEARNS, F.W. 1978. Primary productivity of emergent macrophytes in a Wisconsin freshwater marsh ecosystem. *Am. Midl. Nat.*, **100**: 320-332.

KRUSI B.O. & WEIN, R.W. 1988. Experimental studies on the resiliency of floating *Typha* mats in a freshwater marsh. *J. Ecol.*, **76**: 60-72.

KSENOFONTOVA, T. 1989. General changes in the Matsulu bay reedbeds in this century and their present quality (Estonian SSR). *Aquat. Bot.*, **35**: 111-120.

KVET, J., SVOBODA, J. & FIALA, K. 1969. Canopy development in stands of *Typha latifolia* L. and *Phragmites communis* Trin. in South Moravia. *Hydrobiologia*, **10**: 63-75.

LIEFFERS, V.J. 1983. Growth of *Typha latifolia* in Boreal forest habitats, as measured by double sampling. *Aquat. Bot.*, **15**: 335-348.

LIEFFERS, V.J. & SHAY, J.M. 1982. Seasonal growth and standing crop of *Scirpus maritimus* var. *paludosus* in Saskatchewan. *Can. J. Bot.*, **60**: 117-125.

LINDE, A. F., JANISCH, T. & SMITH, D. 1976. *Cattail: The significance of its growth, phenology and carbohydrate storage to its control and management*. Tech. Bull. 94, Department of Natural Resources, Madison, Wisconsin.

MASON, C.F. & BRYANT, R.J. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, **63**: 71-95.

MCNAUGHTON, S.J. 1966. Ecotypic function in the *Typha* community type. *Ecol. Monogr.*, **36**: 297-325.

MCNAUGHTON, S.J. 1968. Autotoxic feedback in regulation of *Typha* population. *Ecology*, **49**: 367-369.

MCNAUGHTON, S.J. 1975. r- and k- selection in *Typha*. *Am. Nat.*, **109**: 251-261.

MEREZHKO, A.I., SMIRNOVA, N.N. & GORBIK, V.P. 1979. Growth of stands of lesser reedmace (*Typha angustifolia*) and the functioning of its root system. *Hydrobiol. J.*, **15**: 15-19.

MIDDLEMISS, E. 1974. *The Rondevlei Bird Sanctuary. A record of the environment, 1952-1974*. Report for the Divisional Council of the Cape, Cape Town.

NEELEY, R.K. & DAVIS, C.B. 1985. Nitrogen and phosphorus fertilisation of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. 1. Emergent plant production. *Aquat. Bot.*, **22**: 347-361.

NOBLE, J.C., BELL, A.D. & HARPER, J.L. 1979. The population biology of plants with clonal growth. 1. The morphology and structural demography of *Carex arenaria*. *J. Ecol.*, **67**: 983-1008.

O'CALLAGHAN, M. 1980. *Gross production and seasonal changes in standing crop of four species of swamp plants at Rondevlei Bird Sanctuary*. Unpublished report, Botany Department, University of Cape Town, Cape Town.

OGDEN, J. 1981. Studies in the population dynamics of *Typha* at Lake Pukepuke. *N.Z. J. Ecol.*, **4**: 124-125.

PELIKAN, J., SVOBODA, J. & KVET, J. 1970. On some relations between the production of *Typha latifolia* and a muskrat population. *Zool. Listy*, **19**: 303-329.

PENNING DE VRIES, F.W., BRUNTING, A.H.M. & VAN LAAR, H.H. 1974. Products, requirements and effeciency of biosynthesis: a quantative approach. *J. Theor. Biol.*, **45**: 339-377.

PENKO, J.M. & PRATT, D.C. 1985/86. Growth and mortality of shoots in three populations of *Typha glauca* Godr. *J. Minn. Acad. Sci.*, **53**: 25-28.

PRATT, D.C. & ANDREWS, N.J. 1980. Cattails (*Typha* spp.) as an energy source. In: *Energy from Biomass and Waste*. White, J.W., McGrew, W. & Suttor, M.R. (eds). Florida.

REDDY, K.R. & DE BUSK, W.F. 1987. Nutrient storage capabilities of aquatic and wetland plants. In: *Aquatic Plants for Water Treatment and Resource Recovery*. Reddy, K.R. & Smith, W.H. (eds). Magnolia Publishing Inc., New York.

ROBERTS, J. 1987. *The autocology of Typha spp. in South-Eastern Australia*. PhD Thesis, University of Adelaide, Australia

ROBERTS, J. & GANF, G..G. 1986. Annual production of *Typha orientalis* Presl. in inland Australia. *Aust. J. Mar. Fresh. Res.*, **37**: 659-668.

SALZMAN, A.G. & PARKER, M.A. 1985. Neighbours ameliorate local salinity stress for rhizomatous plant in a heterogenous environment. *Oecol.*, **65**: 273-277.

SCHUBAUER, J.P. & HOPKINSON, C.S. 1984. Above- and below-ground emergent macrophyte production and turnover in a Coastal marsh ecosystem, Georgia. *Limnol. Oceanogr.*, **29**: 1952-1965.

SHARMA, K.P. & GOPAL, B. 1977. Studies on stand structure and primary production in *Typha* species. *Int. J. Ecol. Environ. Sci.*, **3**: 45-66.

SHARMA, K.P. & PRADHAN, V.N. 1983. Study on growth and biomass of underground organs of *Typha angustata* Bory. and Chaub. *Hydrobiologia*, **98**: 147-151.

SHAY, J.M. & SHAY, C.T. 1986. Prairie marshes in western Canada, with special reference to the ecology of five emergent macrophytes. *Can. J. Bot.*, **64**: 443-454.

SHINOZAKI, K. & KIRA, T. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *J. Inst. Polytech., Osaka City Univ.*, **12**: 69-82.

SIEGEL, S. 1956. *Non-parametric Statistics for the Behavioral Sciences*. McGraw-Hill, Kogakusha.

SMITH, C.S., ADAMS, M.S. & GUSTAFSON, T.D. 1988. The importance of below-ground mineral element stores in cattails (*Typha latifolia* L.). *Aquat. Bot.*, **30**: 343-352.

SMITH, L.M. & KADLEC, J.A. 1983. Seed banks and their role during drawdown of a North American marsh. *J. Appl. Ecol.*, **20**: 673-684.

TOMLINSON, P.B. 1974. Vegetative morphology and meristem dependence - the foundation of productivity in seagrass. *Aquacult.*, **4**: 107-130.

ULRICH, K.E. & BURTON, T.M. 1985. The effects of nitrate, phosphate and potassium fertilisation on growth and nutrient uptake patterns of *Phragmites australis* Cav. Trin. ex Steudel. *Aquat. Bot.*, **21**: 53-62.

ULRICH, K.E. & BURTON, T.M. 1988. An experimental comparison of the dry matter and nutrient distribution patterns of *Typha latifolia* L., *Typha angustifolia* L., *Sparganium eurycarpum* Engelm. and *Phragmites australis* Cav.) Trin. ex Steudel. *Aquat. Bot.*, **32**: 129-139.

VAN DER TOORN, J. & MOOK, J.H. 1982. The influence of environmental factors and management on *Phragmites australis*. 1. Effects of burning, frost and insect damage on shoot density and shoot size. *J. Appl. Ecol.*, **19**: 477-499.

VAN DER VALK, A.G. 1985. Vegetation dynamics of prairie glacial marshes. In: *The Population Structure of Vegetation*. White, J. (ed.). Dr W. Junk Publishers, The Hague.

VAN DER VALK, A.G. & DAVIS, C.B. 1978. Primary production of prairie glacial marshes. In: *Freshwater Wetlands*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

VAN DER VALK, A.G. & DAVIS, C.B. 1980. The impact of natural drawdown on the growth of four emergent species in a prairie glacial marsh. *Aquat. Bot.*, **9**: 301-322.

WATERS, I. & SHAY, J.M. 1991. A field study of the effects of water depth, order of emergence and flowering on the growth of *Typha glauca* shoots using the Richard's model. *Aquat. Bot.*, **39**: 231-242.

WESTLAKE, D.F. 1975. Primary production of freshwater macrophytes. In: *Photosynthesis and productivity in different environments*. Cooper, J.P. (ed.). Cambridge University Press, Cambridge.

WHITE, J.M. & SINCLAIR, L.R. 1979. Effect of plant spacing on growth and yield of transplanted cattails. *Proc. Soil Crop Sci. Soc. Florida*, **38**: 18-20.

WILLIAMSON, P. 1976. Above-ground primary production of chalk grasslands allowing for leaf death. *J. Ecol.*, **64**: 1059-1075.

*Addition to paragraph 4, page 109.*

Net annual aboveground production (NAAP) was calculated using the Allen Curve Method recommended for *Typha* (Dickerman *et al.*, 1986). This method calculates cohort production graphically as the area beneath a curve relating shoot density and mean shoot biomass over the growing season. The Maximum-Minimum Method, where production is equal to the difference between maximum and minimum biomasss measured during the growing season (Westlake, 1975), was used to estimate net annual belowground production (NABP). Net annual production (NAP) was the sum of NAAP and NABP corrected for rhizome mortality (5% - McNaughton, 1975), and for the translocation of energy stores from the shoot to the rhizome during winter die-back (Roberts & Ganf, 1986). Translocation was estimated from maximum and minimum rhizome standing crop, assuming maximum and minimum starch concentrations of 45 and 7% (Gustafson, 1976), and converting starch to equivalent dry weight using the factor 0.645 (Penning de Vries *et al.*, 1974).

# CHAPTER 5

# THE EFFECT OF FLOOD REGIME ON LITTER PRODUCTION BY, AND DECOMPOSITION OF, *TYPHA CAPENSIS*


## SUMMARY

This study examines the effect of flooding and drought on the decomposition of *Typha capensis* (Rohrb.), a common South African emergent macrophyte. It emphasises the importance of litter formation by fragmentation and shoot collapse in the process of emergent macrophyte decomposition. Demographic methods were used to quantify litter formation while the conventional litter bag method was used to measure weight loss from the detritus or litter layer. Most litter (66%) was produced by leaf fragmentation which began before shoots reached peak biomass. One third of fragmentation losses was recorded prior to shoot death. Shoot collapse was generally delayed for at least two weeks after shoot death and falling shoots accounted for only 30% of fallen litter. The flood regime of the wetland, which controlled moisture availability in the littoral zone, had a significant effect on the rate of shoot collapse and litter decay. Standing litter that was never flooded persisted up to six times longer than that which was permanently flooded. Leaf material decomposed twice as rapidly in areas which were flooded ($k$ = 0.29% day$^{-1}$) than in dry areas ($k$ = 0.13% day$^{-1}$). The results are discussed with reference to methods used to study decomposition and production, and the effect of litter on macrophyte community productivity and demography.


## INTRODUCTION

The decomposition of aquatic macrophyte litter has been described for many species under different environmental conditions (see reviews by Chamie & Richardson, 1978; Davis & van der Valk, 1978a; Godshalk & Wetzel, 1978; Odum & Heywood, 1978; Brinson *et al.*, 1981; Godshalk & Barko, 1985; Belova & Raspopov, 1987). The process of decomposition starts

prior to senescence when bacterial colonisation causes cuticular erosion and peeling (Suberkropp *et al.*, 1976; Howard-Williams & Davies, 1978), which facilitate the rapid leaching of soluble cell components once senescence starts (Howard-Williams & Davies, 1978; Belova & Raspopov, 1987). Microbial decay and mineralisation follow the death of the plant material. Dead material is shed as litter, either by fragmentation or by the collapse of the entire plant (Davis & van der Valk, 1978a). Less is known about the decomposition of belowground materials. However, this is assumed to proceed more slowly than that of aboveground material because physical conditions are less suitable for decay (Chamie & Richardson, 1978; Gallagher, 1978).

The rate of leaching, litter formation and microbial decay are dependent on environmental conditions, especially temperature, oxygen supply and moisture levels (Gallagher, 1978; Howard & Howard, 1979; Pellikaan, 1984; Robarts, 1986). Decomposition rates vary with plant species, with woody ones decomposing more slowly than herbaceous ones, and the more succulent herbs decomposing more rapidly than their fibrous counterparts (Gallagher, 1978).

Past research has generally focused on the processes occurring after litter has been shed, and has neglected the decay of necromass (dead plant material still attached to the live plant) and the formation of litter (e.g. Boyd, 1970, 1971; Mason & Bryant, 1975; Howard-Williams & Junk, 1976; Howard-Williams & Howard-Williams, 1978; Puriveth, 1980; Brock *et al.*, 1985; Hill, 1985; Morris & Lajitha, 1986; Steinke & Ward, 1987). This approach may be satisfactory for submerged and floating-leaved macrophytes, which are generally confined to the aquatic environment during growth and decomposition. It is not, however, suited to the study of emergent macrophytes, parts of which senesce and die in an aerial environment, only subsequently entering the litter-, or detritus-layer

(collectivly referred to as litter-layer hereafter) to complete decomposition (Davis & van der Valk, 1978a,b).

Litter formation by emergents is important because it determines the rate at which material is transferred from the plant to the detritus layer, or from an aerial environment to the sediment surface, with associated change in both the rate and process of decomposition. In a *Typha* marsh, for example, leaching and fragmentation have been shown (Davis & van der Valk, 1978a) to be the principal causes of weight and nutrient loss from necromass; microbial activity only became important after litter had reached the sediment surface. The timing of litter formation is also important because the season determines the physical conditions within the litter layer, and thus the rate of invertebrate fragmentation and microbial decay, at the time of litter fall. Decomposition is likely to be most rapidly completed in systems where litter is produced at a constant rate, or where litter production peaks when conditions favour microbial decay.

Aerial decomposition of aquatic macrophytes has not been totally ignored, but work has generally been of a descriptive nature and has been confined to prairie glacial marshes and to freshwater tidal marshes (Davis & van der Valk, 1978b; Odum & Heywood, 1978; Newell *et al.*, 1989). Little is known about aerial decomposition in other systems, or about the factors which regulate the process (Gallagher, 1978) and, as stated previously, other studies have restricted their attention to litter formation following shoot death (Davis & van der Valk, 1978a,b, 1983; Newell *et al.*, 1989). The role of environmental conditions in controlling and modifying these processes has not been investigated. This study aimed to fill some of these gaps by quantifying litter formation by *Typha capensis* growing in a freshwater marsh. It examines fragmentation losses prior to, and following shoot

death, as well as the decay of litter once it becomes part of the litter-layer. The effect of hydrological regime on shoot collapse and subsequent weight loss is also examined.

## THE STUDY AREA

This study was conducted on the rushbeds (*Typha capensis*) of Rondevlei. The climate, geology and vegetation of the area have been described previously (Chapter 3), with details regarding the morphometry and chemistry of Rondevlei specifically treated in Chapter 4.

*Typha* dominates the littoral zone of Rondevlei, with stands varying in width from 12 to 90m and covering an area of 11.5ha. The rushbeds were generally monospecific, but *Senecio halimfolius* L. is also found along the landward edge of the beds. Rondevlei rushbeds can be divided into three parts on the basis of their demographic structure:

1. An high-shore senile zone, which was dominated by dead, standing shoots and which included no juvenile shoots;
2. A central mature zone, which was dominated by generative shoots, and
3. An low-shore narrow zone, characterised by low shoot density and an equal proportion of juvenile and generative shoots.

These growth phases were respectively associated with areas which were never-, seasonally- and always-flooded (Chapter 4). Flooding depth ranged from a few centimetres in summer, to 1.2m along the inner margin during winter. Soil moisture in the never-flooded zone ranged between 21 and 42%. In the seasonally-flooded area soil moisture fell to a minimum of 42% during summer.

## METHODS

### TRANSFER OF LITTER FROM THE AERIAL TO THE AQUATIC ENVIRONMENT

The rate at which dead material was transferred to the litter layer was measured as the rate of leaf fragmentation and shoot collapse. Only generative shoots (estimated age 12 months) were chosen for study as natural fragmentation during the first season of growth was assumed to be insignificant. All study specimens were located in the mature zone of the rushbed.

Fragmentation rates were quantified using litter bags to collect all litter produced by intact individual growing shoots. At the start of the study 50 shoots were enclosed in nylon mesh bags (2.0 x 1.5m, 2cm mesh) which were supported by internal rods to prevent the bags interfering with shoot growth. Litter from each shoot was collected at monthly intervals when the origin of litter (e.g. entire leaves, leaf tips, litter created by herbivore damage) was noted. On return to the laboratory the litter was rinsed to remove silt, oven dried to constant mass at 60°C and weighed to determine litter production $shoot^{-1}$.

Changes in shoot mass due to fragmentation were assessed by comparing the mass of litter lost against shoot maximum biomass. This was calculated using the model formulated from demographic and phenological data collected from Rondevlei rushbeds (Chapter 4).

The persistence of dead shoots as standing litter was demographically estimated. The emergence, growth, senescence and death of three hundred marked shoots, randomly selected from the three growth phases, was monitored. Each shoot was examined monthly to establish phenological changes so that time to senescence, death and collapse could be calculated. Shoots were classified as live when more than 50% of

leaf material was chlorophyllous, senescent when more than 50% of leaf material had turned brown, and dead when 100% of leaf material was brown.

**DECOMPOSITION ON THE LITTER LAYER**

The rate of litter decay on the litter layer was measured using litter bags. Senescent but intact pairs of leaves were harvested from plants in all three growth phases in early winter, when most shoots had begun to senesce. Culms were excluded from the sample because leaves made up most of shoot biomass (Polisini & Boyd, 1972; Garver *et al.*, 1988). Material was returned to the laboratory where leaves were immediately wiped to remove silt and moisture before being cut into 10cm lengths and placed in mesh bags. Material was not dried prior to filling the litter bags, as is usually done (e.g. Davis & van der Valk, 1978a,b; Morris & Lajitha, 1986), because this affects early decomposition processes, particularly the leaching rate (Rogers & Breen, 1982; Hill, 1985). Litter bags were constructed using 180µm-mesh, with the top surface punctured by 5mm holes to allow invertebrate entry while limiting the loss of fragments (Stewart & Davies, 1989). The 63 bags were sealed and weighed (fresh weight) before they were returned to Rondevlei (within 8 hours) where they were left on the vlei floor at six sites, three in seasonally-flooded, and three in never-flooded areas. The remaining material was subsampled and oven dried to constant mass at 60°C, in order to determine the mean fresh:dry weight ratio of the sample. This was used to calculate the "starting" dry weight of litter in each litter bag from fresh weight measurements.

Replicate bags (three from each flood regime, selected randomly from the different sites) were collected at monthly intervals. On return to the laboratory silt was removed by washing the contents into a 80µm-mesh sieve and animals were removed by hand. The remaining material was oven dried to constant weight at 60°C

before weighing to determine weight loss.

All statistical analyses were performed using Statistical Graphics System (Statistic Graphics Corporation, 1985-1989). Data were used to calculate the monthly and annual mean for fragmentation losses ± one standard error. The rate of shoot collapse was analysed by regression analysis. The data from decomposition experiments were fitted to the simple exponential decay model (Olson, 1963) which assumes that, once leaching is complete, litter decays at a constant rate (Nelson *et al.*, 1990). This takes the form:

$$W_t = W_0 e^{-kt},$$

where $W_t$ represents weight at time t days,
$W_0$ is the initial weight, at time 0 days,
$k$ is the decay coefficient.

## RESULTS

### FRAGMENTATION

Losses of biomass to fragmentation were recorded throughout the study period (September 1987 to August 1989), but they peaked in late summer of both years (Fig. 5.1). During this period, abscised older leaves made up most of the litter. There was a secondary peak in November of both years, corresponding with the start of the summer winds. Damaged leaf tips dominated this litter.

Over the two-year study period fragmentation accounted for an average litter fall of 32.3gDW shoot$^{-1}$. The proportion of biomass fragmented varied significantly between shoots (Kruskal-Wallis test statistic = 3.75; $p<0.05$), ranging between 65 and 91% of maximum shoot biomass. Between 9 and 35% of maximum shoot biomass remained as standing litter a year after shoot death. This represents between 3 and 13gDW shoot$^{-1}$, with a mean of 7.8gDW shoot$^{-1}$ ± 3.5. However, there were fragmentation differences between years. In the first

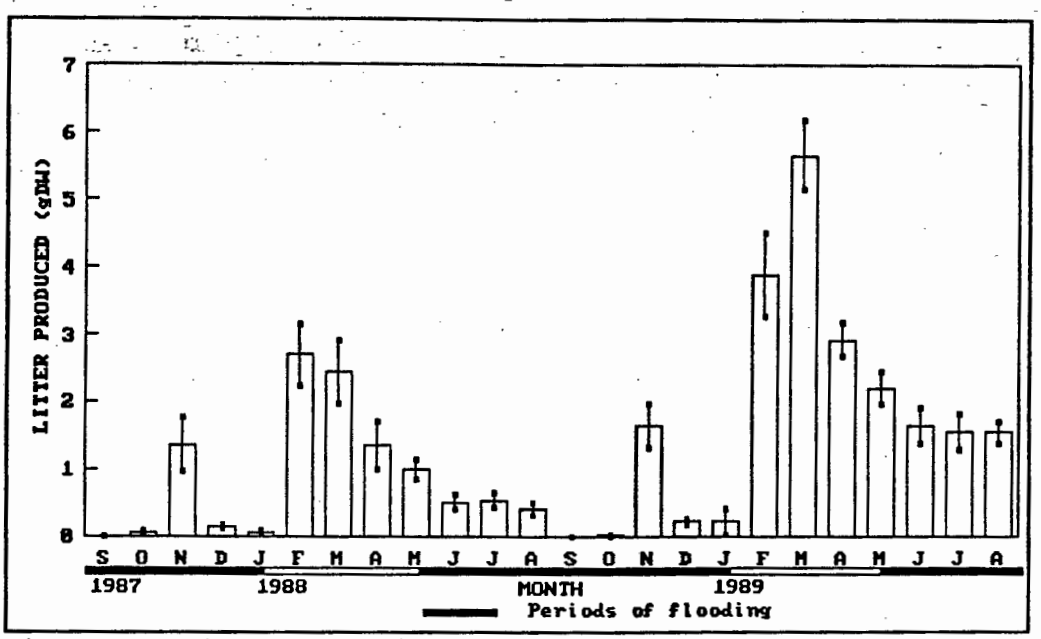



**Figure 5.1** Litter formation by fragmentation in a *Typha* stand. Results are shown as the mean rate of litter formation ± 1 standard error. Solid bars indicate the periods of flooding.

year, fragmentation was approximately half that measured during the second year (Fig. 5.1). The mean annual fragmentation rate was 10.7gDW shoot$^{-1}$ ± 3.0 in 1987/88, and 21.7gDW shoot$^{-1}$ ± 2.7 in 1988/89.

**SHOOT COLLAPSE**

Dead shoots remained part of the rushbed for an average of between 1 and 15 months depending on their position in the rushbed. Shoot collapse was most rapid when shoot bases were always-flooded and slowest when they were never-flooded (Fig. 5.2). The proportion of tagged shoots that had collapsed within 90 days of death were: 100% from the always-flooded zone; 27% of seasonally-flooded shoots, and 0% of never-flooded shoots. It took 390 days for all seasonally-flooded shoots to collapse. At the end of the study, an average of 510 days after their death, 65% of shoots from the never-flooded zone remained standing.

**DECOMPOSITION**

Weight loss was exponential in both wet and dry areas (Fig. 5.3, Table 5.1). Losses from the litter layer

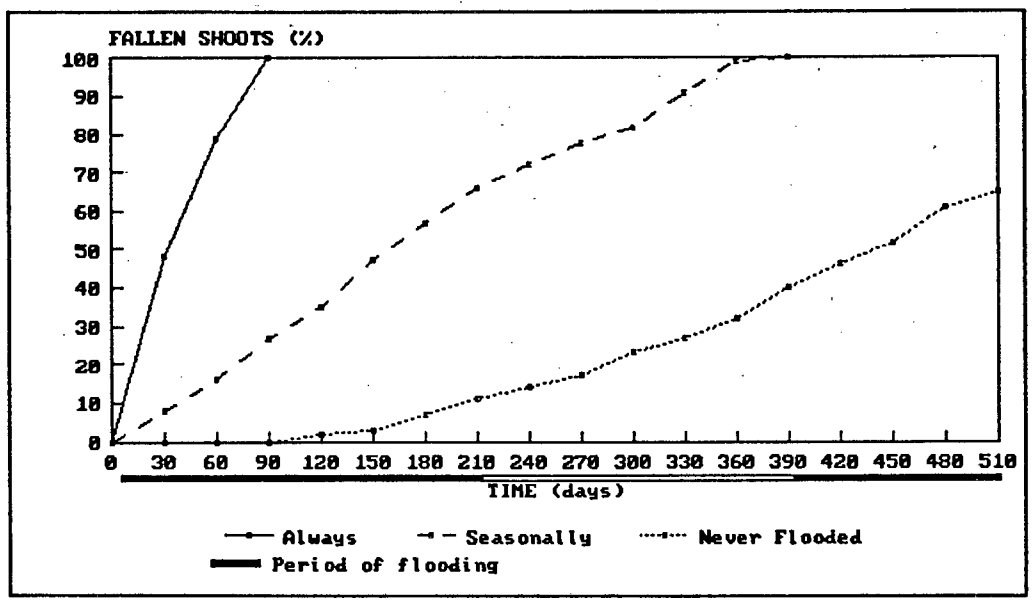



**Figure 5.2:** Seasonal variation in the rate of shoot collapse in a *Typha* stand under different flood regimes. Shaded bars indicate periods of flooding.

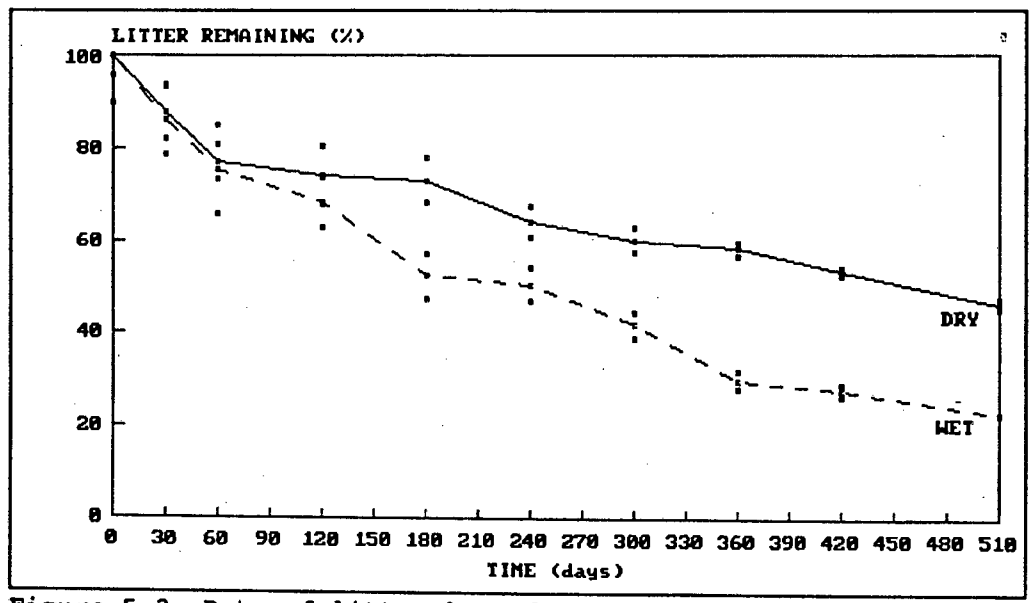



**Figure 5.3:** Rate of litter loss from seasonally-flooded (wet) and never-flooded (dry) parts of a *Typha* stand. (Mean ± 1 standard error).

**TABLE 5.1:** Decay coefficients for *Typha* leaf litter under seasonally-flooded and never-flooded conditions, measured over 510 days.

| FLOOD REGIME | *k* | se | $r^2$ |
|---|---|---|---|
| Seasonally-flooded | 0.0029 | 0.0001 | 0.98 |
| Never-flooded | 0.0013 | 0.0001 | 0.91 |

were relatively low in the dry zone; it took 433 days for a 50% decrease in mass (Fig. 5.3). On the other hand, although weight loss by wet litter was similar to that of dry litter over the first 90 days, decomposition thereafter proceeded more quickly, such that 50% of the original mass was lost in 255 days.

## DISCUSSION

This study supports previous research which has shown that fragmentation is an important component of the decomposition of emergent macrophytes (e.g. Davis & van der Valk, 1978a,b, 1983). Fragmentation was responsible for the transfer of two-thirds of shoot biomass to the litter layer. By contrast, shoot collapse transferred significantly less biomass (30%), especially in areas where dead shoots remained standing for long periods.

The pattern of weight loss by fragmentation following shoot death appears to be related to plant form, life-history, climate and herbivory. Davis & van der Valk (1978b) report that biomass from *Scirpus fluviatilis*, a fragile plant species from the prairie glacial marshes of Iowa, North America was lost during storms due to mechanical damage. Consequently, litter fall was determined by the severity and duration of storms, and varied from year to year. In the same areas, *Typha glauca* was less susceptible to mechanical damage and weight loss tended to be linear as leaves were abscised and leaf tips died, unless shoots were damaged by grazing (Davis & van der Valk, 1978a). Thus, weight loss was similar between years (Davis & van der Valk, 1978a). In *Spartina alterniflora*, where dead leaves do not abscise, 34 to 36% of leaf biomass entered the litter layer as it was shredded by salt marsh periwinkles, while a further 11 to 15% was lost through fungal activity (Newell *et al.*, 1989).

Litter production by *T. capensis* in Rondevlei was seasonal, but there were also annual differences

related to the death of the shoots at the end of their second season. Litter production in juvenile stands was, therefore, lower than in older stands, especially those dominated by senile shoots.

The mass of litter produced by live *Typha* shoots was relatively high: approximately 30% of peak biomass was shed prior to shoot death. This has important implications, for studies of the decomposition of *Typha* have previously examined litter formation only after shoot death. The proportion of shoot biomass shed prior to death may be higher than measured in this study which did not quantify litter formation during the shoots' first season.

The results of this study also show that a significant proportion of shoot production (7% maximum shoot biomass) was lost by fragmentation prior to the shoot reaching peak biomass. This is important with regard to the methodology employed in macrophyte productivity studies, some of which assume no mortality prior to maximum standing crop (e.g. Matthews & Westlake, 1969; Kirby & Gosselink, 1976). If 7% of maximum shoot biomass (38.5gDW) was lost prior to the shoot reaching peak biomass, and shoot density was 36.2 shoots $m^{-2}$ (data from Chapter 4), litter fall would amount to 97.8gDW $m^{-2}$. This is 6% of aboveground production (1 635gDW $m^{-2}$ $yr^{-1}$; Chapter 4). This estimate of *Typha* mortality is lower than most reported values. These were highest in Britain (2 and 23% - Mason & Bryant, 1975; Westlake, 1975), and lower in the warm-temperate regions of South Africa (16% - Howard-Williams, 1980) and Australia (13% - Roberts & Ganf, 1986).

The persistence of dead shoots for two or more years has been reported for other *Typha* stands (Mason & Bryant, 1975; Davis & van der Valk, 1978b). Shoot collapse occurs when the shoot base rots and is unable to support the shoot against physical damage (Davis & van der Valk, 1978a). As decomposition around the shoot base is primarily microbial, it should proceed

most rapidly when conditions are wet, but remain aerobic (Brinson *et al.*, 1981; Hill, 1985; Steinke & Ward, 1987). The higher rate of collapse in the wet zones, compared to that of dry areas may also be due to physical damage (Davis & van der Valk, 1978a; Graneli, 1989), because shoots exposed to wind and wave action collapse sooner than those which are less exposed.

Shoot collapse affects stand productivity because, while the culms remain standing, they physically fill the rushbed. This inhibits the emergence of new shoots and reduces the growth of new shoots due to competition for light and space (Haslam, 1971a,b; Dickerman & Wetzel, 1985; Graneli, 1989). Thus production may have been limited in areas where standing litter densities were high.

The rate at which *Typha* litter decomposes is low by comparison to most aquatic macrophytes (Table 5.2). In general, submerged and floating-leaved macrophytes decompose more rapidly than emergent species such as *Typha* and *Phragmites*. This has been attributed to differences in total fibre content (Godshalk & Wetzel, 1978), but may also reflect differences in C:N and C:P ratios (Howard-Williams & Howard-Williams, 1978; Neeley & Davis, 1985; Almazan & Boyd, 1978). The abundance and activity of invertebrate shredders may also have a profound effect on the rate of decomposition (e.g. Webster & Simmons, 1978; Howard-Williams & Davies, 1979; Camilleri, 1989; Stewart & Davies, 1989), causing site-to-site differences.

In this study the rate at which submerged *Typha* litter decomposed was similar to that recorded in most other temperate wetlands (Table 5.2). Any variations may partially be due to differences in methodology. Litter dried prior to filling the litter bags decomposes more slowly than fresh litter, because drying retards decay after an initial high mass loss

**TABLE 5.2:** Comparison of decomposition rates of various aquatic macrophytes from various localities. To facilitate comparison of different studies rates are given as the time in days for the first 50% of a given mass of material to disappear ($t_{50}$).

| Species | Locality | $t_{50}$ | Reference |
|---|---|---|---|
| *Azolla pinnata* | India | 72 | Kulshreshtha & Gopal, 1982a |
| *Lemna* spp. | UK | 20 | Laube & Wohler, 1973 |
| *Hydrilla verticillata* | India | 35 | Kulshreshtha & Gopal, 1982a |
| *Potamogeton pectinatus* | S.Africa | 35 | Howard-Williams & Davies, 1979 |
| *P. lucens* | Poland | 2.7 | Peicznska, 1972 |
| | USA | 13 | Hill & Webster, 1982 |
| *P. perfoliatus* | Poland | 2.3 | Peicznska, 1972 |
| | USA | 13 | Hill & Webster, 1982 |
| | India | 71 | Kulshreshtha & Gopal, 1982a |
| *P. diversifolius* | UK | 82 | Wohler *et al.*, 1975 |
| *P. crispus* | S.Africa | 172-345 | Rogers & Breen, 1982 |
| | USA | 32 | Hill & Webster, 1982 |
| *Nuphar luteum* | USA | 8-9 | Twilley, 1976 |
| *Salvinia auriculata* | Brazil | 100 | Howard-Williams & Junk, 1976 |
| *Eichhornia crassipes* | Brazil | 10 | Howard-Williams & Junk, 1976 |
| *Paspalum repens* | Brazil | 12 | Howard-Williams & Junk, 1976 |
| *Cynodon dactylon* | S.Africa | 18-28 | Furness & Breen, 1982 |
| *Zizania aquatica* | UK | 90 | Whigham & Simpson, 1977 |
| *Peltandra virginica* | UK | 30 | Whigham & Simpson, 1979 |
| *Juncus effusus* | USA | 90 | Boyd, 1971 |
| *Sparganium eurycarpum* | USA | 571 | Davis & van der Valk, 1978b |
| *Scirpus fluviatilis* | USA | 286 | Davis & van der Valk, 1978a |
| *S. mucronatus* | India | 154-238 | Kulshreshtha & Gopal, 1982b |
| *Phragmites australis* | UK | 200 | Mason & Bryant, 1975 |
| *P. karka* | India | 152 | Kulshreshtha & Gopal, 1982b |
| *Carex rostrata* | Sweden | 150 | Danell & Sjoberg, 1978 |
| *Cladium jamaicense* | USA | 300 | Davis, 1991 |
| *Typha capensis* | S.Africa | 255-433 | This study |
| *T. latifolia* | USA | 180 | Boyd, 1970 |
| *T. domingensis* | Malawi | 93 | Howard-Williams & Howard-Williams,1978 |
| | USA | 180-510 | Davis, 1991 |
| *T. angustifolia* | UK | 361-426 | Mason & Bryant, 1975 |
| *T. angustata* | India | 116 | Kulshreshtha & Gopal, 1982b |
| *T. X glauca* | USA | 482 | Davis & van der Valk, 1978a |

due to accelerated leaching (Furness & Breen, 1982; Rogers & Breen, 1982). Other differences may be due to differences in temperature (Gallagher, 1978; Godshalk & Wetzel, 1978; Brinson *et al.*, 1981; Ogwada *et al.*, 1984), with decomposition rates in Rondevlei being higher than most other temperate areas because conditions were relatively warm. Similarly, temperature differences may also account for the higher rates of *Typha* decomposition reported for tropical wetlands (Howard-Williams & Howard-Williams, 1978; Kulshreshtha & Gopal, 1982b).

Litter exposed to air decomposed more slowly than litter which was seasonally flooded, as has been previously reported (de la Cruz, 1975; Hill, 1985; Steinke & Ward, 1987). This is usually attributed to the role of moisture which promotes rapid leaching of soluble litter components and subsequently enhances the microbial breakdown of refractory compounds, as long as conditions remained aerobic (Godshalk & Wetzel, 1978; Steinke & Ward, 1987; Brinson *et al.*, 1981). Although oxygen concentrations around the litter bags in Rondevlei were not measured, conditions in the well-mixed shallow water body were unlikely to have been anaerobic at any time (e.g. Semmelink, 1990). The fact that the wet litter was intermittently exposed may have also increased the rate of decomposition, because dry periods allow the litter to be colonised by terrestrial invertebrates, increasing fragmentation (Steinke & Ward, 1987).

The decomposition rate constants calculated for this study are low by comparison with results obtained in other studies on the decomposition of *Typha* (Table 5.3). One would, however, expect estimates of rate constants to be sensitive to the time span across which models are fitted (Nelson *et al.*, 1990). They should be highest for short studies because weight loss is most rapid during the first months of decomposition, when the litter is relatively labile and when it may have higher C:N and C:P ratios

**TABLE 5.3:** Comparison of decay coefficients reported for *Typha* spp.

| *k* | Duration of study (days) | Species | Reference |
|---|---|---|---|
| 0.0070 | 56 | *T. capensis* | Hill & Webster, 1982 |
| 0.01 | 60 | *T. glauca* | Nelson *et al.*, 1990 |
| 0.004 | 154 | *T. angustifolia* | Hill, 1985 |
| 0.0035 | 180 | *T. capensis* | Boyd, 1970 |
| 0.002 | 330 | *T. glauca* | Davis & v d Valk, 1978a |
| 0.0019 | 348 | *T. capensis* | Puriveth, 1980 |
| 0.0029 | 310 | *T. capensis* | This study |
| 0.0013 | 310 | *T. capensis* | This study |
| 0.0012 | 525 | *T. glauca* | Davis & v d Valk, 1978b |
| 0.0014 | 525 | *T. glauca* | Brinson *et al.*, 1981 |
| 0.0022 | 527 | *T. glauca* | Brinson *et al.*, 1981 |
| 0.0019 | 626 | *T. angustifolia* | Mason & Bryant, 1975 |

(Howard-Williams & Howard-Williams, 1978; Neeley & Davis, 1985; Almazan & Boyd, 1978; Belova & Raspopov, 1987). When short-term studies (<200 days) are excluded from the comparison, the *k* values for this study lie within the reported range (Table 5.3).

Litter is an important source of food to consumers because it usually has a higher nutritional value than the live plant material (de la Cruz, 1975), but the negative effects of litter persistence on the wetland are considerable. In Rondevlei, litter production in the areas which were never-flooded exceeded the rate of decomposition so that less than 50% of the litter produced each year decomposed in the same period. Weight loss in wet rushbeds was more rapid, and the 715.3gDW $m^{-2}$ produced annually would decompose within a year. These results are in agreement with observations that there was no litter build up in the flooded rushbeds, but that there was a substantial litter layer (10 - 15cm deep) in unflooded zones. In addition to enhancing the rate of sediment accumulation, the litter and standing dead shoots affect the demography of the dry rushbed zone. They shade the rushbed sediments and thus limit stand vigour (McNaughton 1968; Haslam 1971a,b; Sharma & Gopal 1978; Bonnewell *et al.*, 1983). Shading also

prevents the germination of other wetland plants (Grace, 1983; Gryseels, 1989; Thompson & Shay, 1985; Jordan *et al.*, 1990), reducing species diversity and thus environmental heterogeneity in wetland ecosystems (Beule, 1979).

## CONCLUSIONS

1. Fragmentation is an important part of the decomposition of emergent macrophytes, being responsible for the formation of two-thirds of the material entering the litter layer.

2. Losses by fragmentation in *T. capensis* are primarily due to the loss of dead leaves by abscission, or the mechanical damage of leaf tips. Losses by fragmentation increase after the death of the shoot, but are significant even before maximum shoot biomass is reached, and continue for at least one year following shoot death.

3. Dead shoots are persistent, especially in areas where shoot bases are not flooded. Standing litter may inhibit recruitment, reducing stand vigour.

4. Litter decomposes relatively quickly in seasonally flooded areas, but decomposition is at a significantly lower rate in dry areas. In these areas a litter layer accumulates, and this may reduce stand productivity.

## REFERENCES

ALMAZAN, G. & BOYD, C.E. 1978. Effects of nitrogen levels on rates of oxygen consumption during decay of aquatic plants. *Aquat. Bot.*, 5: 119-126.

BELOVA, M.A. & RASPOPOV, I.M. 1987. Macrophytes and their bacterial decomposition in inland waters (review). *Hydrobiol. J.*, 23: 1-7.

BEULE, J.D. 1979. *Control and management of cattails in south-eastern Wisconsin wetlands*. Tech. Bull. No. 112. Dept. Nat. Res., Madison, Wisconsin.

BONNEWELL, V., KOUKKARI, W.L. & PRATT, D.C. 1983. Light, oxygen and temperature requirements for *Typha latifolia* seed germination. *Can. J. Bot.*, **61**: 1330-1336.

BOYD, C.E. 1970. Vascular aquatic plants for mineral nutrient removal from polluted waters. *Econ. Bot.*, **24**: 95-103.

BOYD, C.E. 1971. The dynamics of dry matter and chemical substances in a *Juncus effusus* population. *Am. Midl. Nat.*, **86**: 98-45.

BRINSON, M.M., LUGO, A.E. & BROWN, S. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Ann. Rev. Ecol. System.*, **12**: 123-161.

BROCK, T.C.M., DE LYON, M.J.H., VAN LAAR, E.M.J.M. & VAN LOON, E.M.M. 1985. Field studies on the breakdown of *Nuphar lutea* (L.) Sim. (Nymphaceae) and a comparison of three mathematical models for organic weight loss. *Aquat. Bot.*, **21**: 1-22.

CAMILLERI, J. 1989. Leaf choice by crustaceans in a mangrove forest in Queensland. *Mar. Biol.*, **102**: 453-459.

CHAMIE, J.P.M. & RICHARDSON, C.J. 1978. Decomposition in Northern wetlands. In: *Freshwater Wetlands: Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

DANELL, K. & SJOBERG, K. 1978. Decomposition of *Carex* and *Equisetum* in a northern Swedish lake. Dry weight loss and colonisation by macroinvertebrates. *J. Ecol.*, **67**: 191-200.

DAVIS, C.B. & VAN DER VALK, A.G. 1978a. Litter decomposition in prairie glacial marshes. In: *Freshwater Wetlands: Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

DAVIS, C.B. & VAN DER VALK, A.G. 1978b. The decomposition of standing and fallen litter of *Typha glauca* and *Scirpus fluviatilis*. *Can. J. Bot.*, **56**: 662-675.

DAVIS, C.B. & VAN DER VALK, A.G. 1983. Uptake and release of nutrients by living and decomposing *Typha glauca* Godr. tissue at Eagle Lake, Iowa. *Aquat. Bot.*, **16**: 75-89.

DAVIS, S.M. 1991. Growth, decomposition and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat. Bot.*, **40**: 203-224.

DE LA CRUZ, A. 1975. Proximate nutritive value changes during decomposition of salt marsh plants. *Hydrobiologia*, **47**: 475-480.

DICKERMAN, J.A. & WETZEL, R.G. 1985. Clonal growth in *Typha latifolia*: Population dynamics and demography of the ramets. *J. Ecol.*, **73**: 535-552.

FURNESS, H.D. & BREEN, C.M. 1982. Decomposition of *Cynodon dactylon* (L.) Pers. in the seasonally flooded areas of the Pongolo river floodplain: Pattern and significance of dry matter and nutrient loss. *Hydrobiologia*, **97**: 119-126.

GALLAGHER, J.L. 1978. Decomposition processes: Summary and recommendations. In: *Freshwater Wetlands: Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

GARVER, E.G., DUBBE, D.R. & PRATT, D.C., 1988. Seasonal patterns in allocation and partitioning of biomass and macronutrients in *Typha* spp. *Aquat. Bot.*, **32**: 115-127.

GODSHALK, G.L. & WETZEL, R.G. 1978. Decomposition in the littoral zone of lakes. In: *Freshwater Wetlands: Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

GODSHALK, G.L. & BARKO, J.W. 1985. Vegetative succession and decomposition in reservoirs. In: *Microbial Processes in Reservoirs*. Gunnison, D. (ed.). Dr W. Junk Publishers, Dordrecht.

GRACE, J.B. 1983. Autotoxic inhibition of seed germination by *Typha latifolia*: An evaluation. *Oecol.*, **59**: 366-369.

GRANELI, W. 1989. Influence of standing litter on shoot production in reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *Aquat. Bot.*, **35**: 99-109.

GRYSEELS, M. 1989. Nature management experiments in a derelict reedmarsh. 1. Effect of winter cutting. *Biol. Cons.*, **47**: 171-193.

HASLAM, S.M. 1971a. Community regulation in *Phragmites communis* Trin. I. Monodominant stands. *J. Ecol.*, **59**: 65-73.

HASLAM, S.M. 1971b. Community regulation in *Phragmites communis* Trin. II. Mixed stands. *J. Ecol.*, **59**: 75-88.

HILL, B.H. 1985. The breakdown of macrophytes in a reservoir wetland. *Aquat. Bot.*, **21**: 23-31.

HILL, B.H. & WEBSTER, J.R. 1982. Aquatic macrophyte breakdown in an Appalachian river. *Hydrobiologia*, **89**: 53-59.

HOWARD, P.J.A. and HOWARD, D.M. 1979. Relationship of decomposing litter in relation to temperature and moisture. *Oikos*, **33**: 457-465.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophyte communities of the Wilderness Lakes: Community structure and associated environmental conditions. *J. Limnol. Soc. sth. Afr.*, **6**: 85-92.

HOWARD-WILLIAMS, C. & DAVIES, B.R. 1978. The influence of periphyton on the surface structure of a Potamogeton pectinatus L. leaf (an hypothesis). *Aquat. Bot.*, **5**: 87-91.

HOWARD-WILLIAMS, C. & DAVIES, B.R. 1979. The rates of dry matter and nutrient loss from decomposing *Potamogeton pectinatus* in a brackish south-temperate coastal lake. *Freshwater Biol.*, **9**: 13-21.

HOWARD-WILLIAMS, C. & HOWARD-WILLIAMS, W. 1978. Nutrient leaching from the swamp vegetation of Lake Chilwa, a shallow African lake. *Aquat. Bot.*, **4**: 257-267.

HOWARD-WILLIAMS, C. & JUNK, W.J. 1976. The decomposition of aquatic macrophytes in a floating meadow of a central Amazonian Varzea Lake. *Biogeographica*, **7**: 115-123

JORDAN, T.E., WHIGHAM, D.F. & CORRELL, D.L. 1990. Effects of nutrient and litter manipulations on the narrow leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **36**: 179-191.

KIRBY, C.J. & GOSSELINK, J.G. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. *Ecology*, **57**: 1052-1059.

KULSHRESHTHA, M. & GOPAL, B. 1982a. Decomposition of freshwater wetland vegetation. 1. Submerged and free-floating macrophytes. In: *Wetlands: Ecology and Management*. Gopal, B., Turner, R.E., Wetzel, R.G. & Whigham, D.F. (eds). Nat. Inst. Ecol. and Int. Sci. Publ., Jaipur, India.

KULSHRESHTHA, M. and GOPAL, B. 1982b. Decomposition of freshwater wetland vegetation. 2. Above-ground organs of emergent macrophytes. In: *Wetlands: Ecology and Management*. Gopal, B., Turner, R.E., Wetzel, R.G. & Whigham, D.F. (eds). Nat. Inst. Ecol. and Int. Sci. Publ., Jaipur, India.

LAUBE, H.R. & WOHLER, J.R. 1973. Studies on the decomposition of a duckweed (Lemnaceae) community. *Bull. Torrey Bot. Club*, **100**: 238-240.

MASON, C.F. & BRYANT, R.J. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.*, **63**: 71-95.

MATTHEWS, C.P. & WESTLAKE, D.F. 1969. Estimation of production by populations of higher plants subject to high mortality. *Oikos*, **20**: 156-160.

MCNAUGHTON, S.J. 1968. Autotoxic feedback in regulation of *Typha* population. *Ecology*, **49**: 367-369.

MORRIS, J.T. & LAJITHA, K. 1986. Decomposition and nutrient dynamics of litter from four species of emergent macrophytes. *Hydrobiologia*, **131**: 215-223.

NEELEY, R.K. & DAVIS, C.B. 1985. Nitrogen and phosphorus fertilisation of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. 1. Emergent plant production. *Aquat. Bot.*, **22**: 347-361.

NELSON, J.W., KADLEC, J.A. & MURKIN, H.R. 1990. Seasonal comparisons of weight loss for two types of *Typha glauca* Godr. stands. *Aquat. Bot.*, **37**: 299-314.

NEWELL, S.Y., FALLON, R.D. & MILLER, J.D. 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt-marsh grass *Spartina alterniflora*. *Mar. Biol.*, **101**: 471-481.

ODUM, W.E. & HEYWOOD, M.A. 1978. Decomposition of intertidal freshwater marsh plants. In: *Freshwater Wetlands: Ecological Processes and Management Potential*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

OGWADA, R.A., REDDY, K.R. & GRAETZ, D.A. 1984. Effects of aeration and temperature on nutrient regeneration from selected aquatic macrophytes. *J. Environ. Qual.*, **13**: 239-243.

OLSON, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**: 322-331.

PEICZNSKA, E. 1972. Ecology of the eulittoral zone of lakes. *Ekol. Polska*, **20**: 637-732.

PELLIKAAN, G.C. 1984. Laboratory experiments on eelgrass (*Zostera marina* L.) decomposition. *Netherlands J. Sea Res.*, **18**: 360-383.

POLISINI, J.M. & BOYD, C.E. 1972. Relationships between cell-wall fractions, nitrogen and standing crop in aquatic macrophytes. *Ecology*, **53**: 484-488.

PURIVETH, P. 1980. Decomposition of emergent hydrophytes in a Wisconsin marsh. *Hydrobiologia*, **72**: 231-242.

ROBARTS, R.D. 1986. Decomposition in freshwater ecosystems. *J. Limnol. Soc. sth. Afr.*, **12**: 72-89.

ROBERTS, J. & GANF, G.G. 1986. Annual production of *Typha orientalis* Presl. in inland Australia. *Aust. J. Mar. Fresh. Res.*, **37**: 659-668.

ROGERS, H.K. & BREEN. C.M. 1982. Decomposition of *Potamogeton crispus* L.: The effects of drying on the pattern of mass and nutrient loss. *Aquat. Bot.*, **12**: 1-12.

SEMMELINK, M.M. 1990. *An introduction to the phosphorus dynamics in Rondevlei*. MSc Thesis, Department of Zoology, University of Cape Town, South Africa.

SHARMA, K.P. & GOPAL, B. 1978. Seed germination and occurrence of seedlings of *Typha* species in nature. *Aquat. Bot.*, **4**: 353-358.

STEINKE, T.D. & WARD, C.J. 1987. Degradation of mangrove leaf litter in the St. Lucia Estuary as influenced by season and exposure. *S.A. J. Bot.*, **67**: 323-328.

STEWART, B.A. & DAVIES, B.R. 1989. The influence of different litter bag designs on the breakdown of leaf material in a small mountain stream. *Hydrobiologia*, **183**: 173-177.

SUBERKROPP, K., GODSHALK, G.L. & KLUG, M.J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology*, **57**: 720-727.

THOMPSON, D.J. & SHAY, J.M. 1985. The effects of fire on *Phragmites australis* in the Delta marsh, Manitoba. *Can. J. Bot.*, **63**: 1864-1869.

TWILLEY, R.A. 1976. Phosphorus cycling in Nuphar communities. In: *Primary productivity and mineral cycling in aquatic macrophyte communities of the Chowan River, North Carolina*. Brinson, M. & Davies, G.J. (eds). Water Resources Research Institute Publication, University of North Carolina, North Carolina.

WEBSTER, J.R. & SIMMONS, G.M. 1978. Leaf breakdown and invertebrate colonisation in a reservoir bottom. *Verh. Internat. Verein. Limnol.*, **20**: 1587-1596.

WESTLAKE, D.F. 1975. Primary production of freshwater macrophytes. In: *Photosynthesis and productivity in different environments*. Cooper, J.P. (ed.). Cambridge University Press, Cambridge.

WHIGHAM, D.F. & SIMPSON, R.L. 1977. Growth, mortality and biomass partitioning in freshwater tidal wetland populations of wild rice (*Zizania aquatica* var. *aquatica*). *Bull. Torrey Bot. Club*, **104**: 347-351.

WHIGHAM, D.F. & SIMPSON, R.L. 1979. The distribution of seeds, seedlings and established plants of Arrow Arum (*Peltandra virginica* (L.) Kunth) in a freshwater tidal wetland. *Bull. Torrey Bot. Club*, **106**: 193-199.

WOHLER, J.R., ROBERTSON, D.D. & LAUBE, H.R. 1975. Studies on the decomposition of *Potamogeton diversifolius*. *Bull. Torrey Bot. Club*, **102**: 76-78.

# CHAPTER 6

# THE PHYSICAL AND CHEMICAL CONTROL OF *TYPHA CAPENSIS* IN THE SOUTH-WESTERN CAPE


**SUMMARY**

The efficiency of physical and chemical (herbicidal) methods generally recommended for the control of *Typha* spp. were tested on *T. capensis* in the south-western Cape. Mature, generative stands were subject to: (1) summer or winter cutting, either alone, or in combination with flooding or a covering of *Typha* litter; (2) burning during summer or winter, or (3) herbicidal treatment (Proprop, African Roundup or Proprop with Weedazol), in order to compare their cost efficiency.

The degree of each control method was evaluated by comparing shoot density and growth rate (as changes in height), and rhizome mortality, between treated and untreated areas. Physical control was most successful when shoots were cut and the stubble flooded for at least four months. Cutting in combination with shading inhibited seedling development, but did not reduce the regeneration of cut shoots or shoot emergence; neither did it increase rhizome mortality. Burnt areas were quickly recolonised by the regeneration of some burnt shoots, and by new shoot emergence.

All herbicides tested killed all shoots and most of the rhizomes. Regrowth in herbicided areas took place from undamaged rhizomes. In the short-term herbicides were the most cost-efficient means of controlling *T. capensis*, but the negative effects of chemical pollution of the aquatic environment are considerable. In addition, their cost efficiency falls in the long-term because they have to be reapplied, usually annually.

Cutting and flooding, where stubble was left submerged for at least four months, was the most successful treatment tested. It is, however, labour intensive and is thus costly, making it a viable option only in areas where labour is relatively cheap and readily available. Furthermore, cut shoots must be flooded. This restricts the use of this method to rushbeds that are either naturally flooded for long periods, or to wetlands where water levels can be manipulated.

**It is recommended that, where possible, cutting and flooding should be used in preference to herbicides, because of the negative impact that herbicides may have on wetland ecosystems. Although labour intensive, cutting is preferred because it is environmentally sound, and it could create employment opportunities in the economically depressed areas of the Cape Flats.**

## INTRODUCTION

*Typha capensis* is widespread among the wetlands of the Cape Flats, where it has spread into and between wetlands (Chapter 3). Wetland mismanagement has caused *Typha* encroachment and rushbeds now interfere with wetland circulation and drainage, block access to recreational water bodies and, by replacing less competitive species, reduce habitat diversity with negative effects on wildlife (Langley, 1989; Thornton & Boddington, 1989). As such the plant is considered to be a weed by wetland managers (Chapter 3).

*Typha* species cause similar problems world-wide (Fiala & Kvet, 1971; Weller & Fredrickson, 1974; Beule, 1979; Murkin & Ward, 1980; Kantrud, 1986; Mallik & Wein, 1986; Axelson & Julian, 1988), and there has been a great deal of research into their control (e.g. Nelson & Dietz, 1960; Shekhov, 1974; Linde *et al.*, 1976; Beule, 1979; Murkin & Ward, 1980; Axelson & Julian, 1988; Sharma & Kushwaha, 1990). Currently recommended control methods can be divided into three categories:

1. Physical removal (manual, mechanical or by burning);
2. Chemical (herbicide) control;
3. Environmental manipulation, and
4. Biological control.

The degree of success achieved using these methods varies widely. For example, Nelson & Dietz (1960) found that *Typha* stands needed to be subjected to drought conditions for a minimum of two years in order to eradicate them, while Kuflikowski (1968) reports that all emergent species (including *Typha*) were eradicated when the wetland was drained for several

months. It is clear that treatments are most effective if timed to coincide with periods when plant energy reserves are smallest (Finlayson *et al.*, 1983; Husak *et al.*, 1987), and this phase varies both between sites and seasonally. For this reason recommended methods needed to be tested under local conditions before being implemented on a large scale.

Most research into physical methods of control recommends that *Typha* is cut three times during the growing season. This procedure removes aboveground shoots and kills most of the belowground organs, especially if the stubble is flooded to prevent gaseous exchange between the rhizomes and the air (Sale & Wetzel, 1983). As far as burning is concerned, most effective control can be achieved if fires are set when the sediments around the shoots are dry, especially if the burnt stubble is subsequently flooded (Nelson & Dietz, 1960; Weller, 1975; Beule, 1979; Sale & Wetzel, 1983; Husak *et al.*, 1986; Mallik & Wein, 1986; Jordan & Whigham, 1988).

Herbicidal treatment is sometimes considered to be a cost-efficient method for control, but the risk of contamination, and the trend toward using more natural methods of control has limited their application in recent years (Anderson, 1986).

Glyphosate (N-phosphonomethyl glycine; retail name in South Africa - "African Roundup") and Dalapon (2,2-dichloroproprionic acid; retail name in South Africa - "Proprop") are the most widely recommended herbicides for use on *Typha* spp. (Nelson & Dietz, 1960; Robson, 1967; Corns & Gupta, 1971; Agronomy Division, 1973; Weller, 1975; Konstantinovic & Dimitrijevic, 1981; Muir *et al.*, 1981; Finlayson *et al.*, 1983; Arsenovic *et al.*, 1986; Grace & Harrison, 1986; Axelson & Julian, 1988; Comes & Kelley, 1989). These systemic herbicides are applied to leaves during periods of rapid downward translocation, thus reaching and killing the rhizomes, as well aboveground shoots.

Roundup is generally considered to be the more effective; it is also less costly and less toxic than Proprop (Linker, 1964; Kenago, 1974; Vermeulen & Rankin, 1990). Proprop is sometimes applied in combination with Amitrol (3-amino-1,2,4 triazole; retail name in South Africa - "Weedazol"), because this combination can be used at lower concentrations than single chemical applications, thereby reducing application costs.

Biological control, by muskrat grazing or insect damage, obviously has limited application locally. In the rushbeds of the prairie pothole region of North America muskrat populations are manipulated so that their lodge building activities create open water areas (Pelikan *et al.*, 1970; van der Valk, 1985). Under normal circumstances muskrat activity will not remove rushbeds completely, but it does increase environmental heterogeneity, improving wetlands as wildlife habitat.

Research showing that the development of *Typha* stands is closely linked to water-level fluctuations (van der Valk, 1985), and that regrowth can be prevented by flooding *Typha* shoots (Sale & Wetzel, 1983; Jordan & Whigham, 1988), has lent support to the argument for using water-level fluctuations to control *Typha* growth and spread. As a result, environmental manipulation (flooding or draining) is widely recommended for control in wetlands where water levels can be manipulated (van der Valk & Davis, 1979; Keddy & Reznicek, 1986). Complete control is usually more successful following drawdown and a prolonged drought period (two growing seasons) than by maintaining extended periods of high water level. This is because it is usually impossible to completely flood stands to the required depth in saucer-shaped wetland basins. The development of *Typha* stands can be restricted to small areas and environmental heterogeneity can be maintained by subjecting wetlands to unpredictable hydrological regimes which override moderate, seasonal

fluctuations (Keddy & Reznicek, 1986). Under these circumstances, *Typha* will not be eradicated, but the stands are less likely to be problematic.

The study reported in this chapter was initiated in order to test the effectiveness of physically removing local *T. capensis* stands by cutting or burning at different times, and under different hydrological conditions. The cost-efficiency of physical removal was then compared to that of herbicidal treatment, in order to establish the best means of controlling *T. capensis* over large areas.

## METHODS

This study was conducted at Rondevlei, in rushbeds adjacent to those used for the demographic and decomposition studies described in Chapters 4 and 5. Control treatments, cutting, burning and herbiciding, were applied to stands in the mature, generative growth phase. These stands were dominated by generative shoots, were the most productive part of the *Typha* fringe, and were confined to the seasonally-flooded littoral zone. Limiting tests to this zone was done in order to eliminated bias resulting from growth in areas less suited to the growth of *Typha*.

Treatments were applied using a Latin Square experimental design, with three replicate blocks (25 x 50m) for each treatment, in order to avoid errors due to environmental gradients within the seasonally-flooded zone. Experimental blocks were separated by 2m-wide pathways, along which shoots were cut to ground level. These were maintained throughout the study in an effort to reduce the vegetative expansion of untreated genets into experimental areas.

Control by cutting was tested by manually clearing experimental blocks using machetes, severing shoots as close to the ground as possible (approximately 10 -

20cm), in August (winter) 1987, and also in January (summer) 1988. Three variations of control by cutting were tested:

1. The effect of cutting alone was tested by clearing all litter from the experimental blocks, leaving cut stumps exposed.
2. The effect of control by flooding was measured when cut stubble was flooded to a minimum depth of 2cm above the shoot stumps. After the winter cut, stubble was flooded by seasonal rain for five months. After the summer cut it was only possible to maintain sufficient water depth for six weeks.
3. The possible shading and/or autogenic effect of *Typha* litter on regrowth was tested by covering cut stubble with a 50cm-layer of litter. Litter was provided by the cut shoots which were left intact once severed from their bases.

*Typha* stands were burned in August 1987 (winter) and January 1988 (summer). Because of the difficulties associated with restricting fires to small areas, a single large area (200 x 75m), protected by mown and cleared firebreaks, was burnt on each occasion. The seasonally-flooded part of the treated area was then divided into three separate sections which served as replicates. Areas adjoining the burnt stand were used as controls. It was not difficult to start the fires during summer, when the sediment and the litter layer were relatively dry, but the winter burn had to be fuelled with dry litter. Once lit, the winter burn proceeded slowly by comparison to the hot, rapid burn of the summer treatment.

Chemical control methods were tested by spraying experimental stands with herbicides in late summer (February). Herbicides were applied using knapsack sprayers equipped with T-shaped nozzles. Three herbicidal treatments were tested:

1. Proprop, at 30 kg $ha^{-1}$;

2. Proprop in conjunction with Weedazol, at 20 kg $ha^{-1}$ for Proprop and 10 l $ha^{-1}$ for Weedazol, and
3. Roundup, at 10 l $ha^{-1}$.

The success of control was estimated by comparing aboveground and belowground mortality, and recolonisation rates in treated areas to mortality and recruitment in control areas. Aboveground mortality was expressed as the percentage of standing litter density to total shoot density. Belowground mortality was estimated by measuring the length of live and dead rhizomes from three replicate soil blocks (25 x 25 x 25cm), expressing the dead rhizome length as a percentage of total rhizome length. Recolonisation rate was measured as changes in shoot density and shoot height. These rates were measured in experimental and control blocks approximately monthly until the end of the study.

Results are presented as the mean of three replicates. Differences between treatments were assessed by comparing recolonisation and rhizome mortality during the 15 months following treatment using Kruskal-Wallis Analysis of Variance (Siegal, 1956).

## RESULTS

### PHYSICAL REMOVAL FOR CONTROL

#### Cutting and Clearing

Cutting and clearing *Typha* shoots immediately reduced aboveground shoot density to zero. It was, however, only a short-term solution as regrowth was observed within four to eight weeks, and shoot densities quickly reached 15 shoots $m^{-2}$ (Fig. 6.1). Nevertheless, some degree of control was achieved, as shown by the fact that shoot densities remained below those of control areas for the duration of the study (Fig. 6.1).

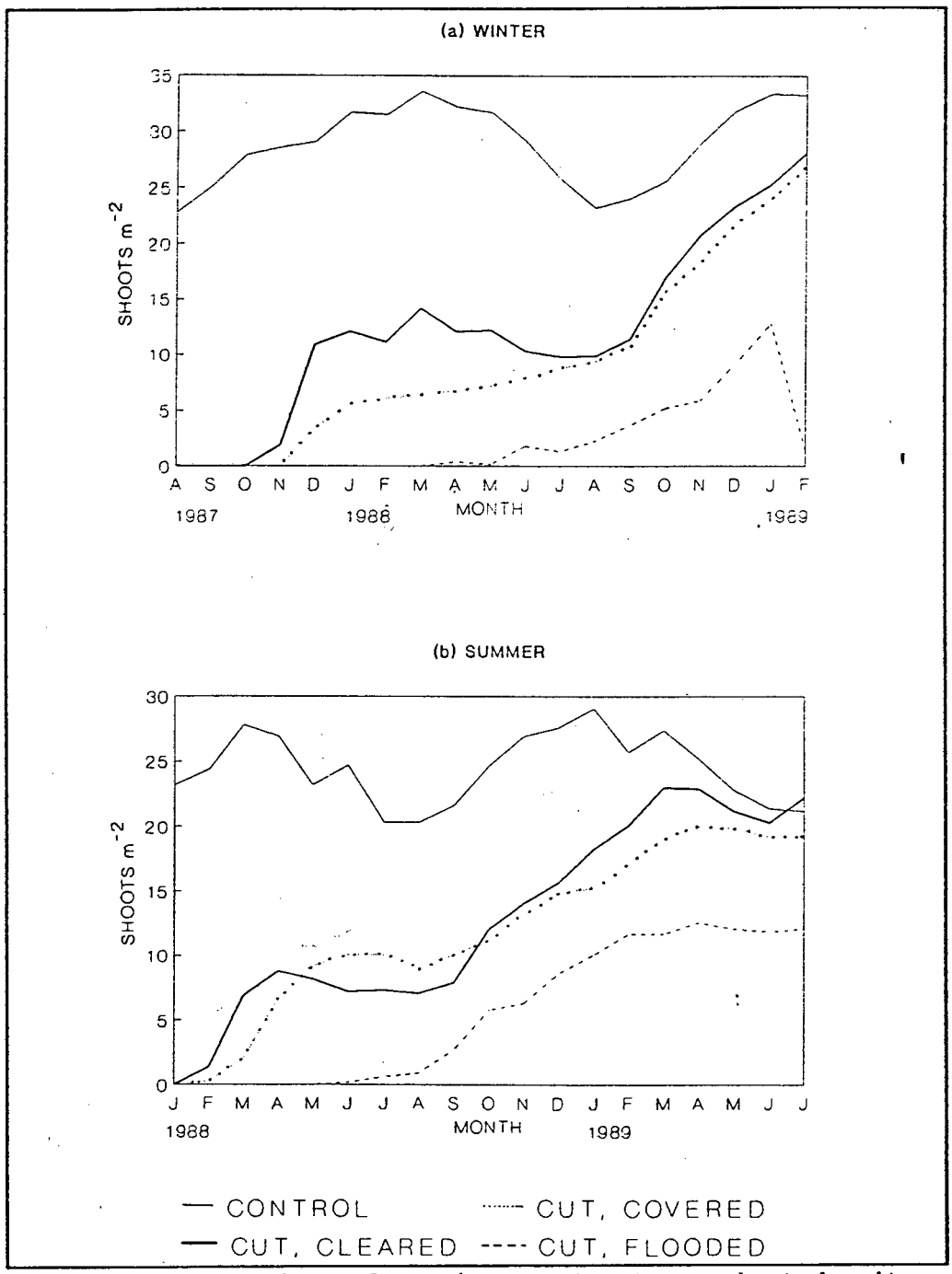



**Figure 6.1: The effect of cutting treatments on shoot density.**

The demography of the regrowth varied according to the season in which cutting was implemented. After a winter cut, most of the regrowth was due to seedling germination and the emergence of sprouts, although there was also some regeneration of cut shoots. After a summer cut, there was no recruitment by seedlings; regrowth was primarily by regeneration of cut shoots, although there was also some new shoot emergence.

The differences in regrowth demography resulted in summer-cut areas being more rapidly recolonised than areas cut during winter, although shoot densities over the period of recolonisation were not significantly different (Table 6.1) After the summer cut, shoot density returned to pre-treatment density within 14 months (Fig. 6.2b). In areas cut during winter, density remained less than those in control areas for at least 18 months (Fig. 6.2a). Cutting and clearing litter is thus an effective, but short-term means of removing problem *Typha* stands. Control would only be maintained if cutting was instituted at least annually.

The growth of shoots, as indicated by changes in height (Fig. 6.2), was enhanced by both treatments; mean monthly height increments were 12.1cm after the winter treatment and 10.0cm during summer, as compared to 3.0cm in untreated areas. Cutting did not cause rhizome death after either summer or winter treatments (Fig. 6.3).

**Cutting and Covering with Litter**

Covering cut shoots with litter after cutting in winter delayed recolonisation by a month (Fig. 6.1a). Shoot density remained below that of uncovered areas for nine months, and was still less than that in control areas by the end of the study (Fig. 6.1a). Shoot densities and growth rates were similar to those recorded in areas without a litter covering (Figs. 6.1 & 6.2; Table 6.1). Regrowth increased in height at an

**Table 6.1:** Results of Kruskal-Wallis Analysis of Variance, comparing shoot densities under different treatments during the 15 months following treatment. C - cut, C&C - cut and cover, C&F - cut and flood; B - Burn; P - Proprop, P&W - Proprop and Weedazol, R - Roundup; S - summer, W - winter. df = 29. Sig. = significance level. * indicates that density was significantly different between treatments at p>0.05.

| TREATMENT 1 | TREATMENT 2 | F | p | Sig. |
|---|---|---|---|---|
| Summer cuts: | | | | |
| S, C | S, C&C | 1.013 | 0.3228 | |
| S, C | S, C&F | 2.15 | 0.1530 | |
| S, C&C | S, C&F | 11.061 | 0.0025 | * |
| Winter cuts | | | | |
| W, C | W, C&C | 2.583 | 0.1192 | |
| W, C | W, C&F | 27.884 | 0.0000 | * |
| W, C&C | W, C&F | 15.181 | 0.0006 | * |
| Herbicides | | | | |
| P | P&W | 0.275 | 0.6098 | |
| P | R | 3.710 | 0.0643 | |
| P+W | R | 3.514 | 0.0681 | |
| Burning | | | | |
| S, B | W, B | 156.868 | 0.0000 | * |
| Summer and winter cuts | | | | |
| S, C | W, C | 0.578 | 0.4617 | |
| S, C&C | W, C&C | 4.467 | 0.0436 | * |
| S, C&F | W, C&F | 5.258 | 0.0296 | * |
| Cuts and burns | | | | |
| S, B | S, C&C | 66.766 | 0.0000 | * |
| S, B | S, C&C | 74.308 | 0.0000 | * |
| S, B | S, C&F | 118.835 | 0.0000 | * |
| W, B | W, C | 23.672 | 0.0000 | * |
| W, B | W, C&C | 11.313 | 0.0022 | * |
| W, B | W, C&F | 4.749 | 0.0379 | * |
| Cuts and herbicides | | | | |
| S, C | P | 17.153 | 0.0000 | * |
| S, C&C | P | 15.795 | 0.0000 | * |
| S, C&F | P | 6.804 | 0.0144 | * |
| W, C | P | 11.181 | 0.0002 | * |
| W, C&C | P | 9.304 | 0.0022 | * |
| W, C&F | P | 0.368 | 0.5556 | |
| Burn and herbicides | | | | |
| S, B | P | 18.594 | 0.0000 | * |
| W, B | P | 21.194 | 0.0000 | * |

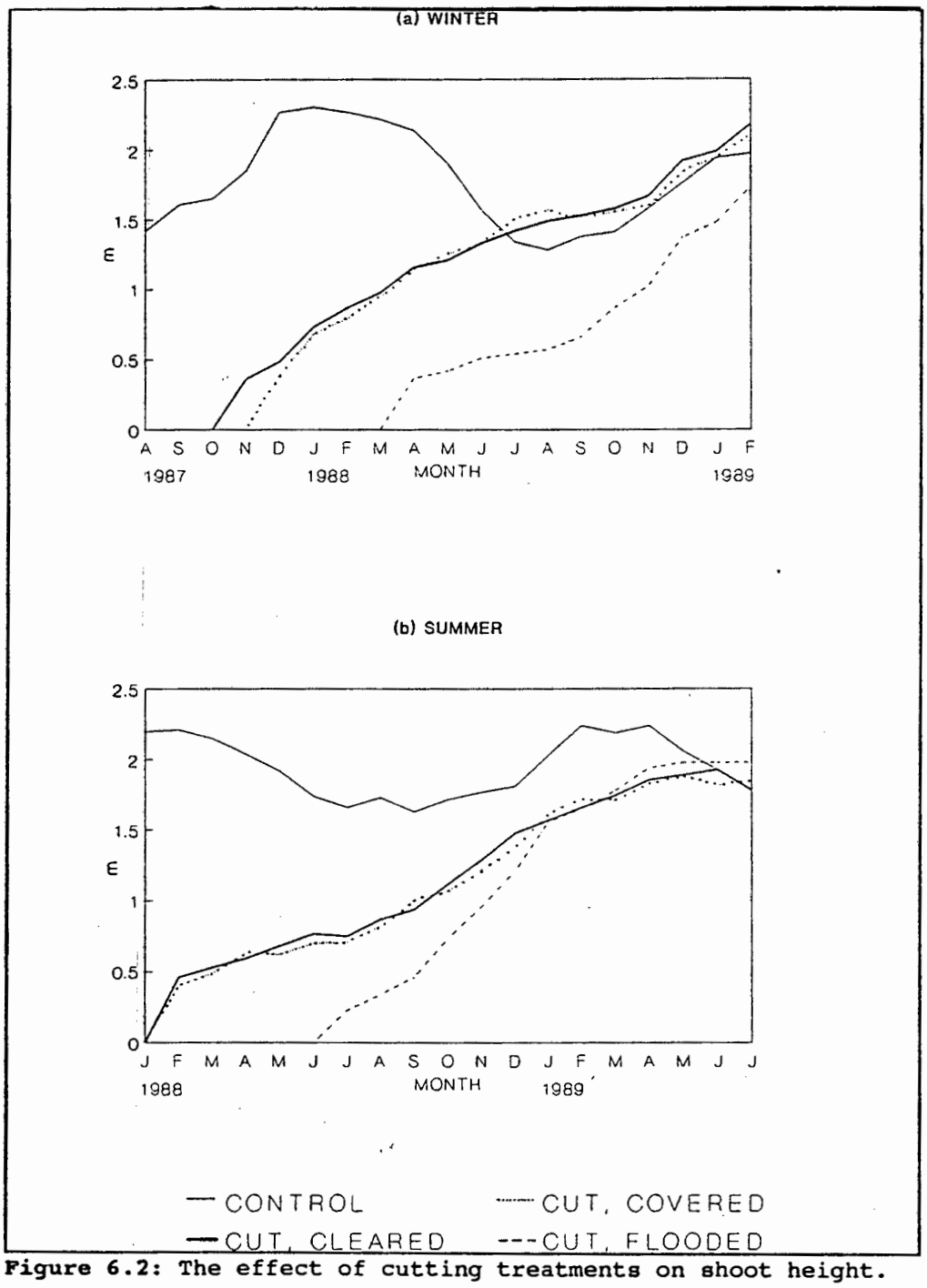



**Figure 6.2: The effect of cutting treatments on shoot height.**

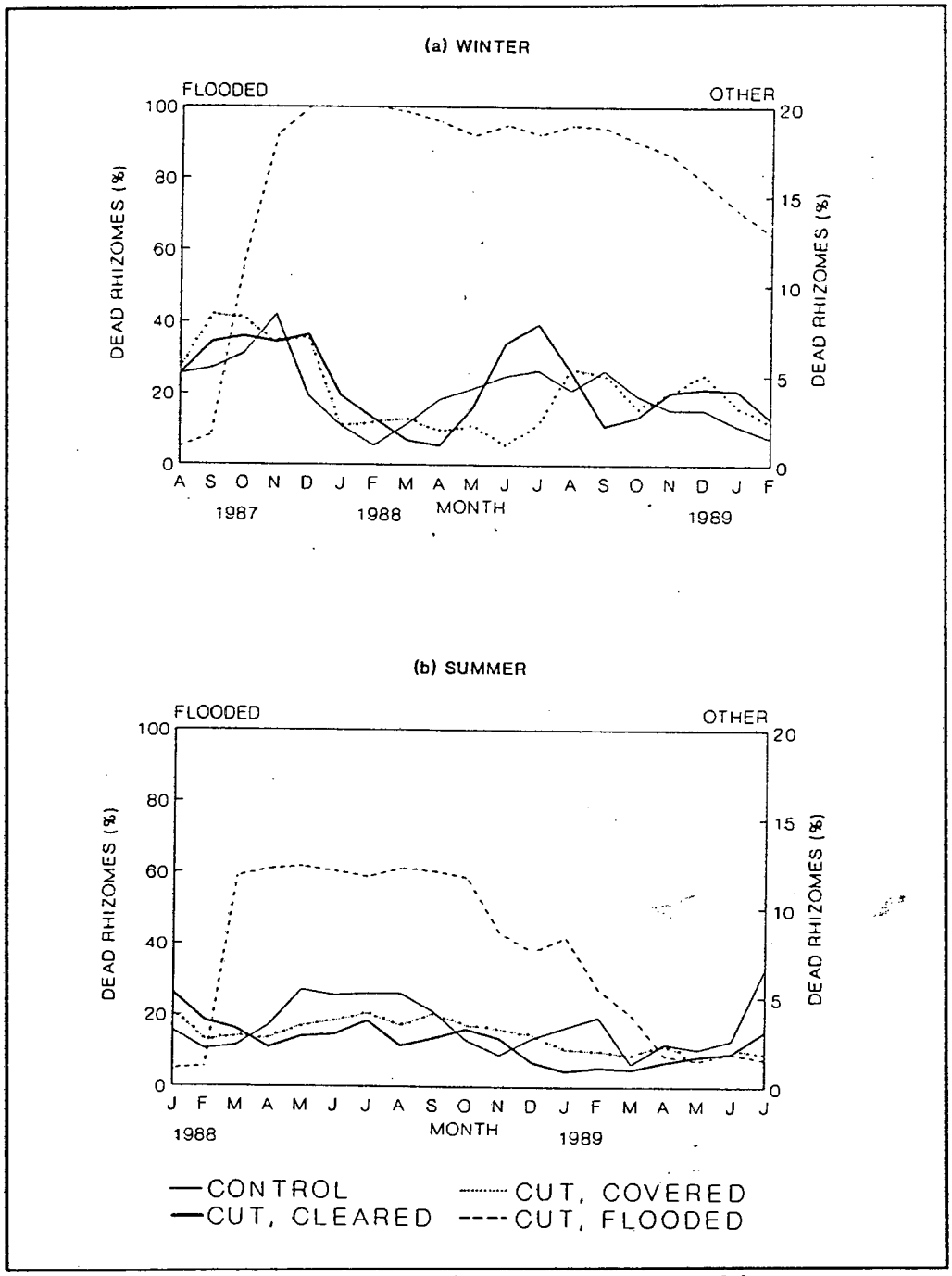



**Figure 6.3: The effect of cutting treatment on rhizome mortality.**

average of 12.2cm month$^{-1}$ (Fig. 6.1a), 10cm faster than that recorded for the control area. The litter cover did not, however, significantly increase rhizome mortality (Fig. 6.3a; Table 6.2).

The litter cover had no additional effect on regrowth and rhizome mortality after summer cutting; shoot density and shoot height were similar in covered and uncovered areas, and rhizome mortality was not significantly different to that of control areas (Figs. 6.1 & 6.2, Table 6.1). Recolonisation was significantly faster in areas treated during summer than those subject to cutting in winter (Table 6.1), where regrowth was only recorded after three months, as opposed to regrowth within a month after the summer cut (Fig. 6.1).

**Cutting and Flooding**

Winter cutting and flooding removed all aboveground evidence of the *Typha* stand for seven months (Fig. 6.1a). New shoots were observed in April 1988, 8 months after treatment. Excavation of 5 quadrats (1m$^2$ x 50cm) showed that the cleared area was being recolonised by vegetative expansion of genets from surrounding, untreated areas. Flooding had no effect on shoot growth, and shoot height was similar in treated and untreated areas by the end of the study (Fig. 6.2a).

Winter cutting and flooding dramatically increased rhizome mortality; all rhizomes in the flooded area had died within four months of treatment (Fig. 6.3a). Remnants of the treated stand (dead cut shoot-bases) had disappeared after ten months. Conversely, the summer cut-and-flood experiment was less successful. Although rhizome mortality did increase during the period when stubble was flooded, only 62% of rhizomes had died when drawdown occurred (Fig. 6.3a). The proportion of dead rhizomes remained high until October 1988, but fell thereafter (Fig. 6.3). The

**Table 6.2** Results of Kruskal-Wallis Analysis of Variance, comparing rhizome mortality under different treatments during the 15 months following treatment. C - cut, C&C - cut and cover, C&F - cut and flood; B - Burn; P - Proprop, P&W - Proprop with Weedazol, R - Roundup; S - summer, W - winter. df = 29. Sig. = degree of significance * indicates that rhizome mortality was significantly different between treatments at p>0.05.

| TREATMENT 1 | TREATMENT 2 | F | p | Sig. |
|---|---|---|---|---|
| Summer cuts: | | | | |
| S, C | S, C&C | 4.026 | 0.0546 | |
| S, C | S, C&F | 65.147 | 0.0000 | * |
| S, C&C | S, C&F | 63.285 | 0.0000 | * |
| Winter cuts | | | | |
| W, C | W, C&C | 0.227 | 0.6426 | |
| W, C | W, C&F | 171.814 | 0.0000 | * |
| W, C&C | W, C&F | 173.482 | 0.0000 | * |
| Herbicides | | | | |
| P | P&A | 0.171 | 0.6871 | |
| P | G | 2.638 | 0.1156 | |
| Summer and winter cuts | | | | |
| S, C | W, C | 11.811 | 0.0019 | * |
| S, C&C | W, C&C | 3.497 | 0.0720 | |
| S, C&F | W, C&F | 26.922 | 0.0000 | * |
| Cuts and herbicides | | | | |
| S, C | P | 637.317 | 0.0000 | * |
| S, C&C | P | 626.061 | 0.0000 | * |
| S, C&F | P | 2.795 | 0.1057 | |
| W, C | P | 540.917 | 0.0000 | * |
| W, C&C | P | 547.437 | 0.0000 | * |
| W, C&F | P | 25.0882 | 0.0000 | * |

increase in live rhizomes was associated with the growth of aboveground biomass, with shoot density reaching 10.1 shoots $m^{-2}$ $yr^{-1}$ after cutting (Fig. 6.1a). Shoot density in flooded areas was, however, still significantly less than that of unflooded and control areas (Table 6.1). Shoot regrowth was due to the regeneration of cut shoots attached to the remaining live rhizomes, rather than to the vegetative expansion of surrounding genets. Shoot growth was not affected by flooding (Fig. 6.2a).

**Burning**

The effect of fire on the appearance of the treated area immediately following treatment varied according to the season in which treatment was instituted. The winter burn removed all traces of standing litter and of the litter layer (Fig. 6.4a). In addition, live shoots were severely damaged by the fire, especially those growing in areas where the water table was below the soil surface. Leaf blades were all burnt, but leaf bases were left virtually intact with only the outer leaves being damaged. Shoots growing in flooded areas were also burnt, but damage was restricted to leaf blades. Leaf sheaths and shoot bases, as well as wet litter, remained untouched by the fire.

After burning in summer, when the water table was low, damage was more severe, with all shoots burnt to the ground. Excavation of small areas indicated that the fire had damaged the root crowns of shoots growing in the driest zones. These organs, lying just below the soil surface, were shrivelled and discoloured. Rhizomes and rhizome buds were not damaged because they lay deeper in the sediments (15 to 20cm below the soil surface). Damage to root crowns and shoot bases became less severe from the terrestrial parts of the stand toward the waterward edge, where soil moisture was relatively high (82% when the fires were lit).

Following the fire set in winter, there was rapid

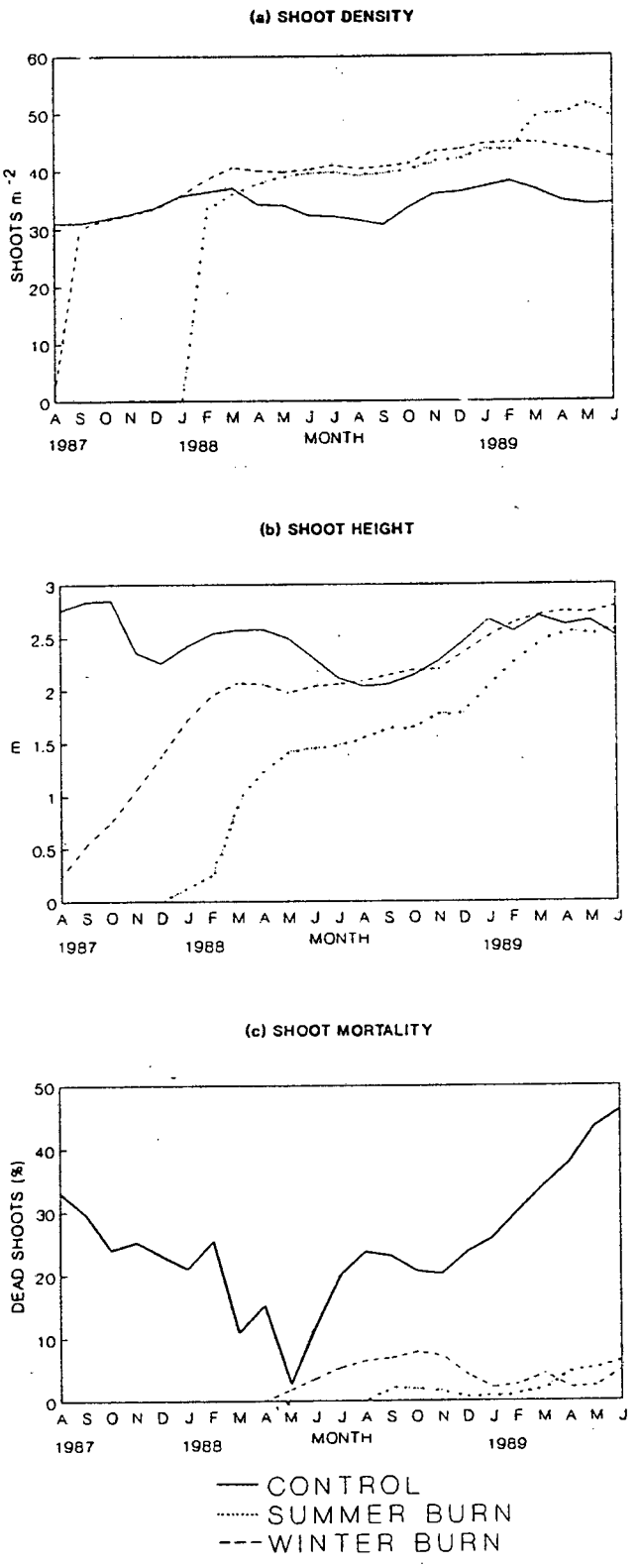



**Figure 6.4:** The effect of burning on (a) shoot density, (b) shoot height and (c) shoot mortality after winter and summer treatments.

regrowth of the burnt shoots from intact bases, as well as emergence of new shoots as sprouts. Shoot density returned to preburn density within one month of treatment, and were considerably higher by the end of the study (burned areas - 42.2shoots $m^{-2}$; control areas - 34.2shoots $m^{-2}$) (Fig. 6.4a). Although shoot height was lower in burned areas for nearly a year after treatment (Fig. 6.4b), rough estimates of standing crop (mean shoot height x mean shoot density) indicate that standing crop was higher in treated areas (117m $m^{-2}$) than in control areas (85.8m $m^{-2}$). These results indicate that treatment stimulated, rather than controlled, *Typha* growth. Winter fires removed all standing litter from the stand, and winter die-back during the next year was low (7.8%) (Fig. 6.4c).

Regrowth following summer burning was also rapid, but was due to emerging sprouts rather than to regeneration of burnt shoots. Shoot densities had reached those of the control areas within a month of treatment, and subsequently exceeded them, peaking at 51.8shoots $m^{-2}$ during the following summer (Fig. 6.4a), confirming that burning stimulated growth. Shoot density after the summer fire was also higher than that in the area burned the previous winter, where maximum shoot density reached 42.6 shoots $m^{-2}$ (Fig. 6.4a; Table 6.1), and the growth rate of emergent shoots was not affected by the fire (Fig. 6.4a). Summer fires removed all standing litter from the treated stands, and shoot mortality in the following winter was low (6.4%). The removal of standing litter reduced total *Typha* shoot density and this was associated with an increase in plant species diversity, with *Zantedeschia aethiopica* becoming common.

Burning caused a decline in flowering frequency of the rushes. None of the regrowth flowered in the summer following winter burning. Flowering in the summer following the summer treatment was also reduced from

14.7% (control) to 3.6%.

Burning was not at all effective as a means of controlling *Typha*, and it appeared to stimulate, rather than inhibit, shoot growth and recruitment. Shoot density increased more rapidly after burning than after cutting, and also resulted in shoot densities exceeding those of control areas (Table 6.1). Burning did, however, reduce seed production, while cutting did not affect flowering frequency.

**CHEMICAL TREATMENT FOR CONTROL**

The effect of herbiciding was apparent almost immediately, with leaves showing signs of chlorosis within one week, although most shoots only died after three to four weeks. None of the treated shoots regenerated (Fig. 6.5a), which indicates that the herbicides effectively killed root crowns. Differences between herbicidal treatments were insignificant (Tables 6.1 & 6.2); all three effectively reduced the density of live shoots to zero, increasing the mortality of aboveground and belowground structures compared to controls (Fig. 6.5).

Live shoots were absent from treated areas until the start of the next growth period (Fig. 6.5a). Regrowth was the product of newly emerged sprouts, rather than germination of seed from the seed bank. Excavation indicated that regrowth was from undamaged rhizomes, not by encroachment from surrounding genets. Regrowth was slow, and by the end of the study live shoot density was still less than 10% of that in the control area (Fig. 6.5a).

Although the herbicides effectively killed most *Typha* shoots, the shoots remained in the wetland as standing litter, the density of which rose to nearly double that of control areas (Fig. 6.5c). Major disadvantages of herbiciding include the facts that

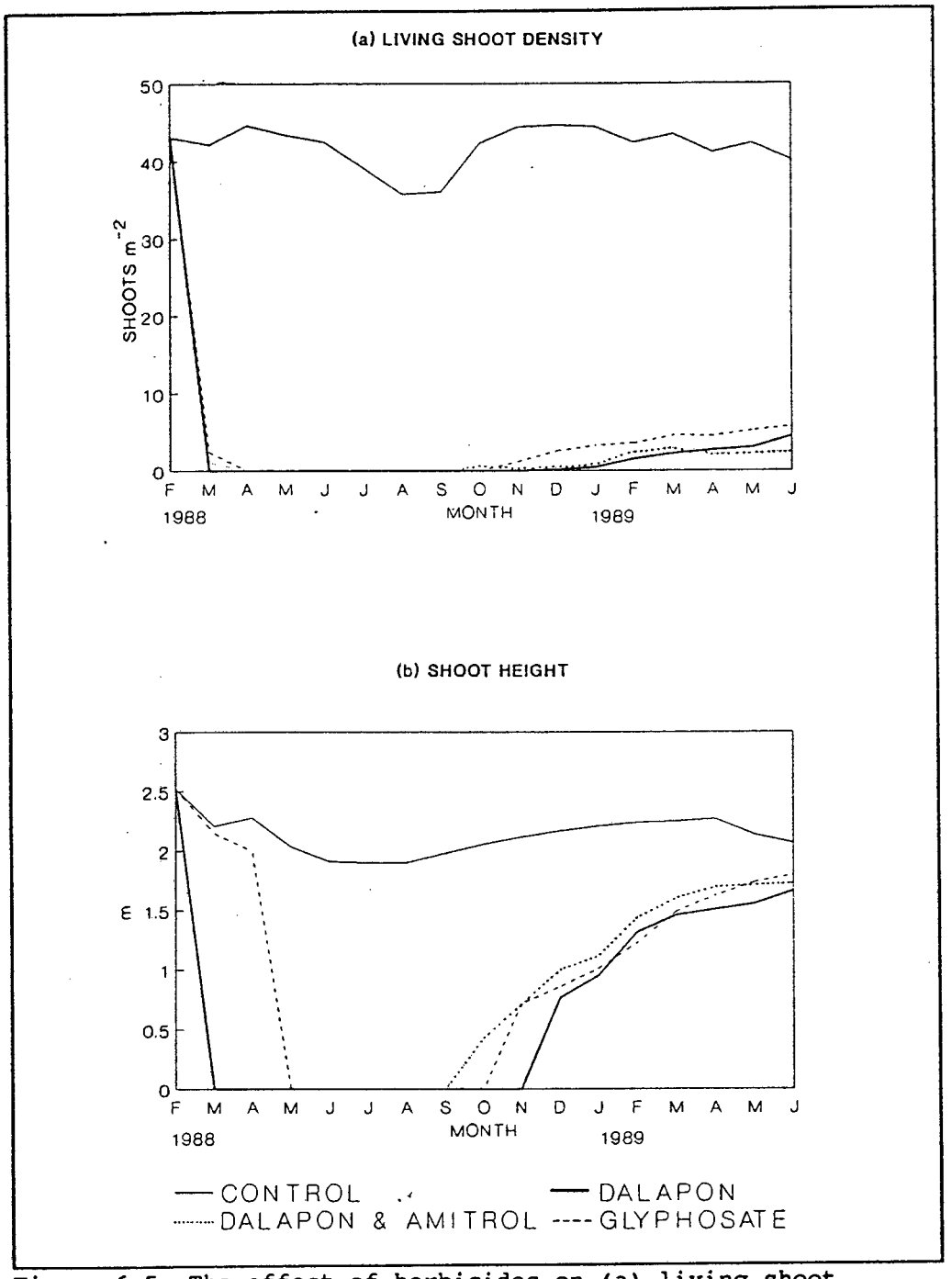



**Figure 6.5:** The effect of herbicides on (a) living shoot density, (b) shoot height, (c) Proportion of dead shoots and (d) rhizome mortality. (continued on next page)

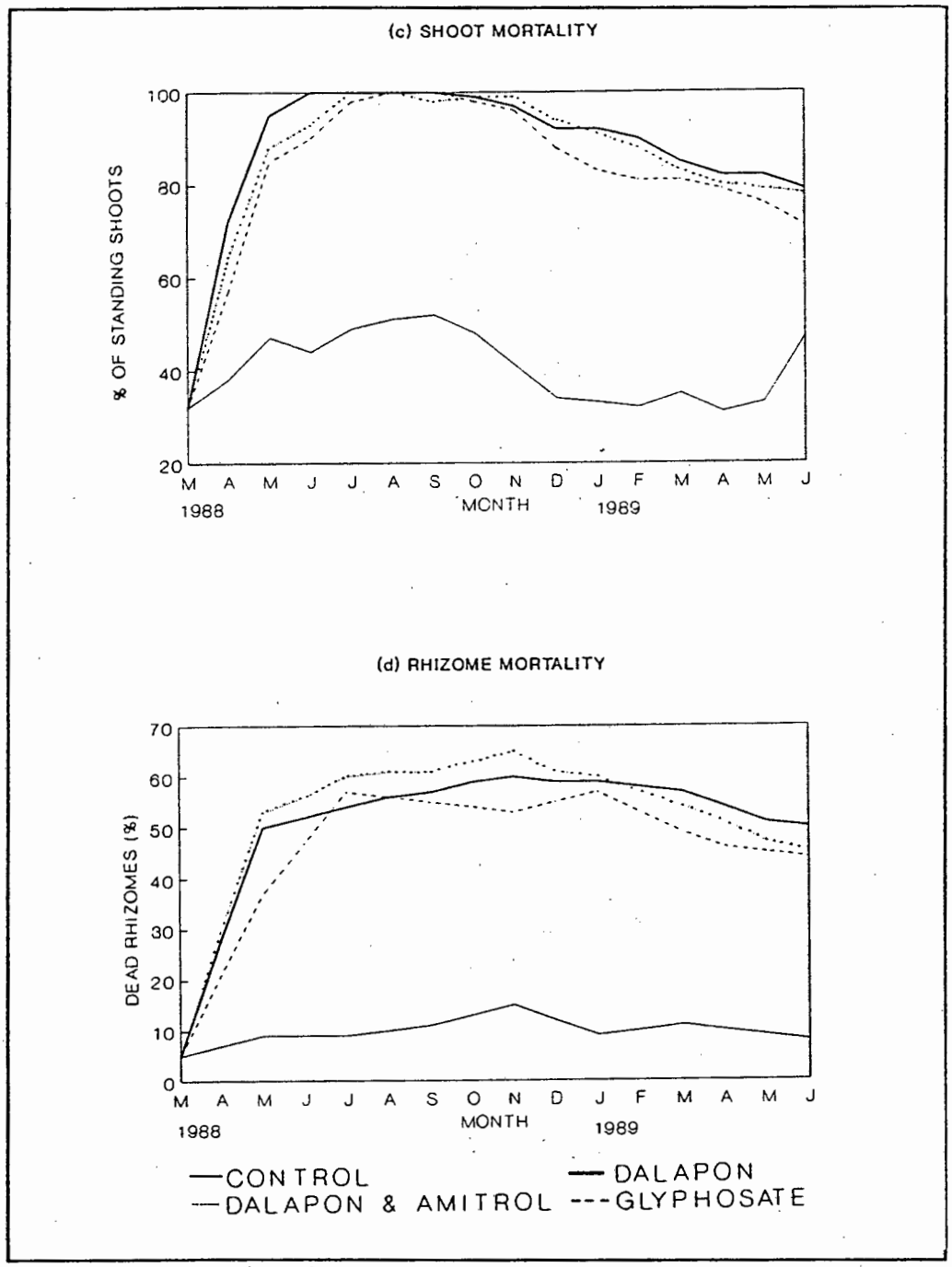



**Figure 6.5** (continued from previous page).

treated areas were more unsightly than controls, they were not utilised by wildlife, and the treated stands were not subject to invasion by other plant species.

Only 30% of rhizomes remained alive after herbiciding (Fig. 6.5d) indicating that rhizome mortality was similar to that recorded after the summer cut-and-flood treatment, but significantly less than that recorded after winter flooding (Table 6.2). This suggests that herbiciding is as effective a long-term control treatment as is prolonged flooding after cutting.

It is interesting to note that there was an eight-week lag between maximum mortality of rhizomes treated with Roundup and those treated with Proprop (Fig. 6.5d), although rhizome mortality over the recovery period was not significantly different between herbicide treatments (Table 6.2). Weedazol did not enhance the effect of Proprop.

## DISCUSSION

### CONTROL BY PHYSICAL REMOVAL

#### Cutting

A single cut above water level did not reduce *Typha* growth or density in this study. This supports previous observations that indicate that a single cut above water level may be counter-productive as removing litter rejuvenates the stand (Sharma, 1978; Ogden, 1981; Sharma & Kushwaha, 1990). The efficiency of control by cutting without flooding may be increased to as high as a 90% reduction in shoot density (Corns & Gupta, 1971) if treatment is repeated at frequent intervals during the growth period, but there are no reports of complete control after cutting alone (Agronomy Division, 1973; Shekhov, 1974; Husak *et al.*, 1986).

Many studies have shown that clearing wetland margins creates an environment suitable for *Typha* seedling establishment (Sharma, 1978; Ogden, 1981; Bonnewell *et al.*, 1983; Sharma & Kushwaha, 1990). This appeared to have been the case in this study where the area cleared in winter was rapidly colonised by species represented in the seed bank. Summer treatment areas, being subject to drought conditions imposed by drawdown, were not recolonised in a similar manner. Instead, some shoots utilised energy stores to regenerate while, where apical dominance was removed, new shoots sprouted. Germination rates were reduced by covering the cleared areas with a mat of *Typha* litter, a result similar to that reported by Szczepanska (1971, 1977), Sharma & Gopal (1978, 1979), Grace (1983), van der Valk (1986) and Ball (1990). These authors attribute the effect of litter to either the release of allochemical inhibitors, or to interference with germination and seedling establishment by shading.

Covering the cut shoot bases with a layer of litter did not improve control (Table 6.1 & 6.2) because it did not reduce recruitment by inhibiting shoot emergence. This result is similar to that reported by van der Valk (1986). Furthermore, although it had the labour-saving advantage of not having to remove and dispose of the litter, it did not take cognisance of the fact that the litter was unsightly and persistent (Chapter 5). In addition, nutrients in decomposing litter simply re-enter the system (Davis & van der Valk, 1983; Cary & Weerts, 1984; Gopal & Sharma, 1984; Reddy & deBusk, 1987; Smith *et al.*, 1988; Jordan *et al.*, 1990; Davis, 1991), where as litter removal would reduce nutrient loading.

In this study cutting in combination with flooding was the most effective way of controlling *Typha* growth by physical means tested in this study. This was because flooding killed the rhizomes by preventing aeration via the shoots (Jordan & Whigham, 1988). When oxygen

levels in the rhizome reach zero (after approximately 8hrs), ethanol, which causes tissue breakdown, is produced by anaerobic respiration (Sale & Wetzel, 1983). The degree of tissue breakdown, which is dependent on the length of time that the shoot is submerged, determines whether or not the entire ramet will die (Murkin & Ward, 1980). The success of treatment thus depends on the submergence of cut shoots long enough to cause rhizome death. In this study that period was four months.

Cutting and flooding have been used widely and effectively for *Typha* management (Nelson & Dietz, 1960; Agronomy Division, 1973; Shekhov, 1974; Weller, 1975; Murkin & Ward, 1980; Sale & Wetzel, 1983; Grace & Harrison, 1986) Control in these studies has been more effective than that reported here. For example, Weller (1975) estimated that regrowth after four years was only 1%. Various authors have recommended that control may be improved by a second, or even third cut in order to ensure that regrowth remains below the water surface (Finlayson *et al.*, 1983; Grace & Harrison, 1986) as even dead shoots are able to supply rhizomes with oxygen (Beule, 1979; Sale & Wetzel, 1983; Jordan & Whigham, 1988). Others have added that digging up the rhizomes by ripping or ploughing (Nelson & Dietz, 1960; Beule, 1979) enhances control. Treatment is most simple if shoots can be cut below the water surface, eliminating the need for reflooding.

It has been shown that cutting is most effective if shoots are first cut when their total non-structural carbohydrate reserves are lowest (Linde *et al.*, 1976; Beule, 1979; Krusi & Wein, 1988). This critical period lies within the two weeks between pistillate spathe emergence and anthesis, which is during December and January in the south-western Cape (Chapter 4). Reserves are lowest when the spikes are green, and are beginning to accumulate when the spikes turn brown (Linde *et al.*, 1976). Other

recommendations include cutting when vegetative shoots reach between 75 and 95% of their final height (Krusi & Wein, 1988), or when 10 to 20% of shoots are flowering (Agronomy Division, 1973). During the study reported here, all cues indicated that cutting should occur in November but, as Linde *et al.*, (1976) have observed, the actual date can vary from year to year due to seasonal variation. The changeover from using, to accumulating, reserves is very rapid (Linde *et al.*, 1976), so treatment programmes should be flexible enough to allow cutting to start as soon as these changes become apparent.

The major disadvantage of cutting is expense which is due either to its manpower requirements or to capital investment. In this study cutting was performed by hand: working in up to 1m of water, it took an average of 500 man-hours to clear 1ha of rushbed. Even at the minimum wage (R2.00 $hr^{-1}$ at the time of treatment), this would usually be considered too costly (R1 000 $ha^{-1}$) to be considered a viable management option, but under local conditions, where there is large-scale unemployment and a huge unskilled workforce, this option remains viable. When cheap labour is unavailable, cutting needs to be mechanised.

In areas where water levels can be controlled, or where drawdown is sufficient to allow *Typha* beds to dry out completely, tractors can be used to slash shoots and to rake up litter. Rear-mounted slashers tend to pass over rushes flattened by the tractor tyres, so side-mounted sicklebars are more effective (Ball, 1990). Sickle-bars cut closer to the ground than rotary mowers, making the shoots easier to flood, and can also be drawn by smaller, lighter tractors, which are more suited to working in muddy conditions. Even when using this type of machinery, however, cutting is slow, and therefore costly (Ball, 1990). Murkin & Ward (1980) report that it took two men with tractors three weeks to cut and clear 2.4ha of rushbed.

Where it is not possible to dry out the rushbed sediment, specialised machinery, able to operate in mud, or in very shallow water, will be necessary. Experimental cutting in Utah used a tractor fitted with steel half-tracks (Nelson & Dietz, 1960). In Minnesota, a specialised floating barge, equipped with counter-rotating screws, was used to cut the shoots at the water-soil interface (D.D. Biesboer, Botany Department, University of Minnesota, pers. comm.). A similar machine was used in the Wilderness lakes to control *Phragmites* (Dr. A.K. Whitfield, J.L.B. Smith Institute of Ithchyology, Grahamstown, pers. comm.). Disadvantages of these machines are that it is difficult to regulate the level at which cutting takes place, they do not remove the cut material from the vlei, and both capital investment and running costs are high (Bagnall 1985; Bagnall *et al.*, 1987; van der Toorn *et al.*, 1990). In addition, mechanisation is both destructive of habitat and disturbing to wildlife, making it unsuitable for areas such as Rondevlei, a waterfowl sanctuary. Finally, this approach, while suited to technically advanced countries such as the USA, is too specialised to suit local demands. In southern Africa, control methods which utilise the large, unskilled workforce should be adopted, because the money saved on capital investment and specialised machinery running costs can be used to generate employment.

**Burning**

Burning marsh vegetation releases nutrients locked in plant biomass, and opens both the canopy and the detritus layers (Kantrud, 1986). The effect of burning emergent vegetation depends on the temperature and intensity of the fire. These generally vary seasonally, with wet burns (winter fires in the south-western Cape) being less destructive than dry (summer) ones. This is largely due to the relative volume of litter and green plant material available, as well as to the water depth and soil moisture levels. As a

result, winter and spring fires open up the canopy, enhancing plant regrowth, while hotter, summer fires burn right into the rootcrowns, killing shoots (Thompson & Shay, 1985).

The increase in live shoot density and decrease in shoot height recorded after burning in Rondevlei was typical of the effect of fire on emergent macrophytes such as *Phragmites* and *Typha* elsewhere (Thompson & Shay, 1985; Turner, 1987). It has been shown that live shoot density may increase because shade-inhibition is lifted by litter removal (Sharma, 1978; Ogden, 1981; Sharma & Kushwaha, 1990). It may also be due to the release of auxiliary bud dormancy by fire damage of terminal buds (Thompson & Shay, 1985). The production of many new shoots, late in the season, which would have depleted the rhizome energy stores, could account for the decline in flowering frequency recorded in this study.

In Rondevlei, the removal of *Typha* stands by burning is not suitable for long-term control, but fire could be used as an effective management tool because previous research has shown that burning at regular intervals rejuvenates senile stands (Weller, 1975) by removing litter (Kantrud, 1986), increasing shoot nutritive value (Smith & Kadlec, 1985; Smith, 1989) and promoting plant diversity (Auclair *et al.*, 1976; Mallik & Wein, 1986; Thompson & Shay, 1989).

Burning may also be used to improve the efficiency of other control methods. Burning stands prior to further treatment reduces shoot densities and removes litter, making it easier either to cut or to spray the regrowth. Following treatment, a second burn can be used to remove litter created by cutting or herbiciding. To avoid nutrient leaching from cut shoots, litter should be burnt as soon as possible after treatment. This technique is not be suitable for areas where there are populations of birds, or for areas close to residential or industrial development.

**CONTROL BY CHEMICAL TREATMENT**

Herbicidal treatment reduced *Typha* growth significantly during the year following application, although there was some regrowth during the following spring. Regeneration is usually reported following a single application of herbicides, and control is generally only maintained by respraying at regular intervals (Gopal, 1986; Comes & Kelley, 1989). Thus, although a single application of herbicides was the cheapest method of control tested, with treatment costing between R375 and R506 $ha^{-1}$ (excluding machinery and labour costs), for control to be maintained, these costs would have to be incurred annually.

Chemical treatment, like manual removal, is most effective if it is timed to coincide with the translocation of photosynthate to renew rhizome stores (Linde *et al.*, 1976). During this study, this period coincided with the most windy time of the year, making it impossible to safely apply herbicides. For this reason spraying was delaying by two months, until the winds had died down. Nevertheless, treatment was still successful, indicating that as long as the stand is sprayed before winter die-back, when translocation stops completely, control is possible. This observation is supported by the results of Comes & Kelley (1989), who found that Roundup was most effective when applied when seeds were mature, rather than when shoots were in full bloom or during anthesis.

Herbicidal treatments were the only control measures tested that did not remove litter from the study site. This proved to be a disadvantage because litter remained standing for the duration of the study, an unsightly grey mass which caused similar problems to those reported for live *Typha* stands: preventing access to the water, blocking drainage and reducing habitat variation. The planning of this type of control should, therefore, also make provision for

litter removal, increasing its cost further.

Roundup is the herbicide most widely recommended in the countries where it is registered (Australia - Finlayson *et al.*, 1983; Axelson & Julian 1988; U.S.A. - Comes & Kelley, 1989), being cheaper, effective at lower concentrations, and less toxic than Proprop (Table 6.3). Other advantages include the rapid rate at which it is inactivated both in soil, and in water, and the fact that it is essentially not toxic to mammals and birds (Carlisle & Trevors, 1988). Unfortunately, fish and invertebrates are sensitive to the herbicide in its commercial form, because of the surfactants in the formula (Carlisle & Trevors, 1988). At recommended field rates, however, Roundup should not have adverse effects on aquatic wildlife (Tooby, 1985, cited in Carlisle & Trevors, 1988). Advocates of Roundup as a means of controlling aquatic macrophytes stress that the risk of contamination is minimised by the affinity of soil particles for Roundup, which bind and inactivate the compound. Thus, they say, should Roundup enter the water at high concentrations, it can be inactivated by stirring up the sediment in the area of contamination (Finlayson *et al.*, 1983). This argument does not consider the different binding properties of soils, making contamination more likely in areas with sand, rather than clay, sediments. Furthermore, while stirring up the sediments may reduce Roundup concentrations, it will also have an adverse affect on the flora and fauna of the area.

Despite the advantages of using Roundup rather than Proprop, only Proprop may be used in South African wetlands under present legislation (Vermeulen & Rankin, 1990). It is relatively "environmentally friendly", being less toxic to aquatic organisms than are many other herbicides, and it is relatively quickly degraded by micro-organisms (Kenaga, 1974). Nevertheless there are risks associated with its use in wetlands: residues do accumulate in aquatic animals

and plants; there is evidence that degradation is slow under some circumstances (e.g. soils of low organic matter concentrations); Proprop is relatively mobile, making it readily leached through soils, and it is only easily degraded by acclimated cultures of bacteria.

**Table 6.3:** Some important characteristics of herbicides tested during trials for the control of *T. capensis*. Oral $LD_{50}$ and Dermal $LD_{50}$ for rats in mg active ingredient $kg^{-1}$ body mass; Inhalation $LD_{50}$ for rats in mg active ingredient $l^{-1}$ $hr^{-1}$. (from Kenaga, 1974; Vermeulen & Rankin, 1990)

| | Proprop | Weedazol | Roundup |
|---|---|---|---|
| Oral $LD_{50}$ | | | |
| - rats | 7700 | 1100-24600 | 4320 |
| - fish (ppm) | 1000 | | |
| Dermal $LD_{50}$ | | | |
| - rats | >3100 | >10000 | >7940 |
| - fish (ppm) | 1000 | | |
| Inhalation LD50 | >200 | 21-200 | 21-200 |

Despite assurances that, when used correctly, there should be no hazardous side effects from chemical use (Bartley & Gangstad, 1974; Grace & Harrison, 1986), it seems that the negative impacts of herbicides on aquatic ecosystems are only relative: some are more damaging than others, but the risk of contamination and environmental disturbance are always incurred. Even short-term exposure to herbicides can have a negative effect on aquatic community structure (e.g. Goldsborough & Robinson, 1986), and the indirect effects of treatment may be considerable (Brooker & Edwards, 1975; Mitchell, 1986). They include:

- perturbation of the oxygen-carbon dioxide balance;
- nutrient release following plant death;
- reduced ecosystem productivity;
- reduced biodiversity, and
- the loss of habitat or food resources for other organisms.

The indirect effects are those which cause the

greatest difference between herbicidal and cutting treatments: plants die *in situ* and regrowth is limited or much reduced, having negative effects on the plant and animal communities (Robson & Barrett, 1977; Brooker & Edwards, 1975). Until there is a greater understanding of the hazardous and more subtle long- and short-term effects of herbicides on aquatic ecosystems, chemical treatment should be restricted to water bodies where cutting-and-flooding is not possible.

If herbicides are the only viable means of controlling *Typha*, it is important that the following precautions are taken to prevent the possible contamination of water and vegetation around the shoots:

1. Recommended dosages should not be exceeded;
2. Chemicals must be applied only until the leaves are wet, not to the point of runoff;
3. Shoots should be sprayed using a foaming nozzle, which decreases runoff and drift, and increases spray adhesion (Axelson & Julian, 1988);
4. Only products approved for aquatic systems after testing by a recognised control body, such as the UK Pesticides Safety Precautions Scheme, should be used (Spencer-Jones, 1986).

## CONCLUSIONS

1. Cutting was successful as a long-term means of control only when the stubble was subsequently submerged for at least four months.

2. Shading of areas that had been cleared by cutting delayed recolonisation by seedlings and by newly emerged buds, but did not inhibit the regeneration of cut-shoot stumps.

3. Cutting was the most expensive management option tested, but it was also the most effective means of control if used in combination with flooding. Under local socioeconomic conditions, it is recommended that cutting is done manually, creating jobs for the many unemployed, unskilled workers in the area, rather than mechanising the process.

4. Burning *Typha* stands removed litter, reducing total shoot density and clearing sediments. This increased the stands' potential as wildlife habitat. It also made it easier to move through the stand, making fire a useful pretreatment to cutting or herbiciding.

5. Roundup and Proprop successfully reduced *Typha* growth for a year, but stands would have to be resprayed annually to prevent reinvasion. Herbicides were the most cost efficient means of control tested, but their use in aquatic ecosystems is not recommended in light of the danger of contamination and environmental disturbance.

**REFERENCES**

AGRONOMY DIVISION, 1973. Cumbungi - a menace to water storage. *Tas. J. Agric.*, 13: 86-90.

ANDERSON, L.W.J. 1986. Recent developments and future trends in aquatic weed management. *Proceedings of the 7th Symposium on Aquatic Weeds, European Weed Research Society,* Loughborough, England.

ARSENOVIC, M., DIMITRIJEVIC, M. & KONSTANTINOVIC, B. 1986. Control of aquatic weeds with herbicides in drainage systems of the Danube-Tisa-Danube in Yugoslavia. *Proceedings of the 7th International Symposium on Aquatic Weeds,* European Weed Research Society, Loughborough, England.

AUCLAIR, A.N.D., BOUCHARD, A. & PAJACZ-KOWSKI, J. 1976. Productivity relations in a *Carex*-dominated ecosystem. *Oecol.*, **26**: 9-31.

AXELSON, S. & JULIAN, C. 1988. Weed control in small dams. Part 1. Introduction: Control of algae and of cumbungi. *Queensland Agric. J.*, **July-Aug**: 241-246.

BAGNALL, L.O. 1985. Biomass harvesters: A new challenge for equipment designers. *Agric. Engin.*, **66**: 16-17.

BAGNALL, L.O., SCHERTZ, C.E. & DUBBE, D.R. 1987. Harvesting and handling biomass. In: *Aquatic Plants for Water Treatment and Resource Recovery*. Reddy, K.R. & Smith, W.H. (eds). Magnolia Publishing Inc, New York.

BALL, J.P. 1990. Influence of subsequent flooding depth on cattail control by burning and mowing. *J. Aquat. Plant Mngmt.*, 28: 32-36.

BARTLEY, T.R. & GANGSTAD, E.O. 1974. Environmental aspects of aquatic plant control. *J. Irrig. Drain. Div.*, **100**: 231-244.

BEULE, J.D. 1979. *Control and management of cattails in south eastern Wisconsin wetlands*. Tech. Bull. No. 112. Dept. Nat. Res., Madison, Wisconsin.

BONNEWELL, V., KOUKKARI, W.L. & PRATT, D.C. 1983. Light, oxygen and temperature requirements for *Typha latifolia* seed germination. *Can. J. Bot.*, **61**: 1330-1336.

BROOKER, M.P. & EDWARDS, R.W. 1975. Aquatic herbicides and the control of water weeds. *Water Research*, **9**: 1-15.

CARLISLE, S.M. & TREVORS, J.T. 1988. Glyphosate in the environment. *Water, Air and Soil Pollution*, **39**: 409-420.

CARY, P.R. & WEERTS, P.G.J. 1984. Growth and nutrient composition of *Typha orientalis* as affected by water temperature and nitrogen and phosphorus supply. *Aquat. Bot.*, **19**: 105-118.

COMES, R.D. & KELLEY, A.D. 1989. Control of common cattail with post-emergence herbicides. *J. Aquat. Plant Mngmt.*, 27: 20-23.

CORNS, W.S. & GUPTA, R.K. 1971. Chemical control of cattail *Typha* latifolia. *Can. J. Plant Sci.*, **51**: 491-497.

DAVIS, C.B. & VAN DER VALK, A.G. 1983. Uptake and release of nutrients by living and decomposing *Typha glauca* Godr. tissue at Eagle Lake, Iowa. *Aquat. Bot.*, **16**: 75-89.

DAVIS, S.M. 1991. Growth, decomposition and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. *Aquat. Bot.*, **40**: 203-224.

FIALA, K. & KVET, J. 1971. Dynamic balance between plant species in South Moravian reedswamps. In: *The Scientific Management of Animal and Plant Communities for Conservation*. Duffey, E. & Watt, A.S. (eds). 11th Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford.

FINLAYSON, C.M., ROBERTS, J., CHICK., A.J. & SALE, P.J.M. 1983. Biology of Australian weeds. II. *Typha domingensis* Pers. and *Typha orientalis* Presl. *J. Aust. Inst. Aust. Weeds*, **49**: 3-10.

GOLDSBOROUGH, L.G. & ROBINSON, G.G.C. 1986. Changes in periphytic algal community structure as a consequence of short herbicidal exposures. *Hydrobiologia*, **139**: 177-192.

GOPAL, B. 1986. Problems of aquatic weeds and approaches to their management in South Asia.In: *Proceedings of the 7th International Symposium on Aquatic Weeds*. European Weed Research Society, Loughborough, England.

GOPAL, B & SHARMA, K.P. 1984. Seasonal changes in concentration of major elements in the rhizomes and leaves of *Typha elephantina* Roxb. *Aquat. Bot.*, **20**: 65-73.

GRACE, J.B. 1983. Autotoxic inhibition of seed germination by *Typha latifolia*: An evaluation. *Oecol.*, **59**: 366-369.

GRACE, J.B. & HARRISON, J.S. 1986. The biology of Canadian weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha glauca* Godr. *Can. J. Plant Sci.*, **66**: 361-379.

HUSAK, S., KVET, J. & PLASENCIA FRAGA, J.M. 1987. Experiments with mechanical control of *Typha* spp. stands. In: *Proceedings of the 7th International Symposium on Aquatic Weeds*. European Weed Research Society, Loughborough, England.

JORDAN, T.E. & WHIGHAM, D.F. 1988. The importance of standing dead shoots of the narrow-leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **29**: 319-328.

JORDAN, T.E., WHIGHAM, D.F. & CORRELL, D.L. 1990. Effects of nutrient and litter manipulations on the narrow leaved cattail, *Typha angustifolia* L. *Aquat. Bot.*, **36**: 179-191.

KANTRUD, H.A. 1986. *Effects of vegetation manipulation on breeding waterfowl in Prairie wetland - a literature review*. Fish and Wildlife Technical Report 3. Washington D.C.

KEDDY, P.A. & REZNICEK, A.A. 1986. Great lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. *J. Great Lakes Res.*, **12**: 25-36.

KENAGO, E.E. 1974. Toxicological and residue data useful in the environmental safety evaluation of Dalapon. *Res. Rev.*, **53**: 109-151.

KONSTANTINOVIC, B. & DIMITRIJEVIC, M. 1981. A contribution to the study of the effectiveness of herbicides against some emergent weed species in the Danube-Tisa-Danube hydrological system. *Zbornik Radova, Poljoprivrednog Fakulteka u Osijeku*, **7**: 127-132.

KRUSI B.O. & WEIN, R.W. 1988. Experimental studies as the resilience of floating *Typha* mats in a freshwater marsh. *J. Ecol.*, **76**: 60-72.

KUFLIKOWSKI, T. 1968. Vegetation of the Goczalkowice Dam reservoir in the years 1964-1966. *Acta Hydrobiol.*, **10**: 165-178.

LANGLEY, C.H. 1989. Problems caused by *Typha*. In: *Typha: Its status, problems, economic benefits and control*. van Warmelo, W. (ed.). Botanical Society of South Africa. Cape Town.

LINDE, A. F., JANISCH, T. & SMITH, D. 1976. *Cattail: The significance of its growth, phenology and carbohydrate storage to its control and management*. Tech. Bull. 94. Department of Natural Resources, Madison, Wisconsin.

LINKER, H. 1964. The design of herbicides. In: *The physiology and biochemistry of herbicides*. Audus, L.J. (ed.). Academic Press, London.

MALIK, A.U. & WEIN, R.W. 1986. Response of a *Typha* marsh to draining, flooding and seasonal burning. *Can. J. Bot.*, **64**: 2136-2143.

MITCHELL, D.S. 1986. The impacts of aquatic weed control on aquatic ecosystems. *Proceedings of the 7th International Symposium of Aquatic Weeds*, European Weed Research Society, Loughborough, England.

MUIR, D.C.G., PITZE, M., BLOUW, A.P. & LOOCKHART, W.L. 1981. Fate of terbutryn in macrophyte-free and macrophyte-containing farm ponds. *Weed Res.*, **21**: 59-70.

MURKIN, H.R. & WARD, P. 1980. Early spring cutting to control cattail in a northern marsh. *Wildl. Soc. Bull.*, **8**: 254-256.

NELSON, N.F. & DIETZ, R.H. 1960. *Cattail control methods in Utah*. Utah State Department of Fish and Game Publication No. 66-2.

OGDEN, J. 1981. Studies in the population dynamics of *Typha* at Lake Pukepuke. *N.Z. J. Ecol.*, **4**: 124-125.

PELIKAN, J., SVOBODA, J. & KVET, J. 1970. On some relations between the production of *Typha latifolia* and a muskrat population. *Zool. Listy*, **19**: 303-329.

REDDY, K.R. & DE BUSK, W.F. 1987. Nutrient storage capabilities of aquatic and wetland plants. In: *Aquatic Plants for Water Treatment and Resource Recovery*. Reddy, K.R. & Smith, W.H. (eds). Magnolia Publishing Inc.

ROBSON, T.O. 1967. Accurate aerial applications of Dalapon to drainage ditches in Britain. *Down to Earth*, **Fall**: 12-14.

ROBSON, T.O. & BARRETT, P.R.F. 1977. Review of effects of aquatic herbicides. In: *Ecological Effects of Herbicides*. Perring, F.H. & Mellanby, K. (eds). Academic Press, London.

SALE, P.J. & WETZEL, R.G. 1983. Growth and metabolism of *Typha* species in relation to cutting treatments. *Aquat. Bot.*, **15**: 321-334.

SIEGAL, S. 1956. *Non-parametric statistics for the Behavioural Sciences*. New York.

SHARMA, K.P. 1978. Effect of cutting on the growth and flowering behaviour of *Typha elephantina* Roxb. *Current Sci.*, **47**: 275-276.

SHARMA, K.P. & GOPAL, B. 1978. Seed germination and occurrence of seedlings of *Typha* species in nature. *Aquat. Bot.*, **4**: 353-358.

SHARMA, K.P. & GOPAL, B. 1979. Effect of water regime on the growth and establishment of *Typha angustifolia* seedlings. *Int. J. Ecol. Environ. Sci.*, **5**: 69-74.

SHARMA, K.P. & KUSHWAHA, S.P.S. 1990. Effects of cutting above-ground organs of *Typha angustata* Bory and Chaub on its growth and total chlorophyll content. *Aquat. Bot.*, **36**: 293-296.

SHEKHOV, A.G. 1974. Effect of cutting time on the renewal of stands of reed and cattail. *Hydrobiol. J.*, **10**: 45-48.

SMITH, C.S., ADAMS, M.S. & GUSTAFSON, T.D. 1988. The importance of below-ground mineral element stores in cattails (*Typha latifolia* L.). *Aquat. Bot.*, **30**: 343-352.

SMITH, L.M. 1989. Effects of grazing and burning on the nutritive quality of cattail in Playar. *J. Aquat. Plant Mngmt.*, **27**: 51-53.

SMITH, L.M. & KADLEC, J.A. 1985. Fire and herbivory in a Great Salt Lake marsh. *Ecology*, **66**: 259-265.

SPENCER-JONES, D.H. 1986. Some problems facing the manufacturers and users of aquatic herbicides in Britain. *Proceedings of the 7th International Symposium of Aquatic Weeds*, European Weed Research Society, Loughborough, England.

SZCZEPANSKA, W. 1971. Alleopathy among the aquatic plants. *Pol. Arch. Hydrobiol.*, 18: 17-30.

SZCZEPANSKA, W. 1977. The effects of the remains of helophytes on the growth of *Phragmites communis* Trin. and *Typha latifolia* L. *Ekol. Pol.*, 25: 437-445.

THOMPSON, D.J. & SHAY, J.M. 1985. The effects of fire on *Phragmites australis* in the Delta marsh, Manitoba. *Can. J. Bot.*, 63: 1864-1869.

THOMPSON, D.J. & SHAY, J.M. 1989. First-year response of a *Phragmites* marsh community to seasonal burning. *Can. J. Bot.*, 67: 1448-1455.

THORNTON, J.A. & BODDINGTON, G. 1989. Problems associated with the bulrush, *Typha latifolia* in Cape Town. In: *Typha: Its status, problems, economic benefits and control*. van Warmelo, W. (ed.). Botanical Society of South Africa, Cape Town.

TURNER, M. G. 1987. Effects of grazing by feral horses, clipping, trampling and burning on a Georgia salt marsh. *Estuaries*, 10: 54-60.

VAN DER TOORN, J., VERHOEVEN, T.A.A & SIMPSON, R.L. 1990. Freshwater marshes. In: Wetlands and Shallow Water Continental Water Bodies. Vol.1. Natural and human relationships. Pattern, B.C., Jorgensen, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

VAN DER VALK, A.G. 1985. Vegetation dynamics of prairie glacial marshes. In: *The Population Structure of Vegetation*. White, J. (ed.). Dr W. Junk Publishers, The Hague.

VAN DER VALK, A.G. 1986. The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. *Aquat. Bot.*, 24: 13-26.

VAN DER VALK, A.G. & DAVIS, C.B. 1979. A reconstruction of the recent vegetational history of a Prairie marsh, Eagle Lake, Iowa, from its seed bank. *Aquat. Bot.*, 6: 29-51.

VERMEULEN, J.B. & RANKIN, J. 1990. *A guide to the use of herbicides*. 12th Edition. Department of Agricultural Development, Republic of South Africa.

WELLER, M.W. 1975. Studies of cattail in relation to management for marsh wildlife. *Iowa State J. Res.*, 49: 383-412.

WELLER, M.W. & FREDERICKSON, L.H. 1974. Avian ecology of a managed glacial march. *Living Bird*, 12: 269-291.

# CHAPTER 7

# GENERAL DISCUSSION AND RECOMMENDATIONS FOR THE CONTROL AND MANAGEMENT OF *TYPHA CAPENSIS* IN CAPE FLATS WETLANDS

*Typha* has always been present in the vleis of the Cape (Martin, 1968; Scott & Bonnefille, 1986), serving as an important part of the ecosystem by providing refuge, breeding areas and food for a large variety of bird species. Without the pressure of urban development, rushbeds were an important component of local wetlands, which were considered wilderness areas, and were used for sailing and fishing. As the south-western Cape was developed, however, the vleis were subjected to greater use and their water levels were stabilised to facilitate this. The manipulation of wetland hydrology, together with the increase in eutrophication due to catchment development, enhanced the growth potential of *Typha*. The stands consequently spread, causing management problems.

Explosive expansion of plant populations is not uncommon, but solutions have usually only been sought when dealing with alien species (i.e. species not indigenous to the area). The question whether or not invasions by alien organisms are fundamentally different from the rapid and extensive increase in range and numbers exhibited by indigenous species, has rarely been addressed. It was alluded to by Elton (1958, cited in Macdonald, 1991), and briefly discussed by Macdonald (1991) in his thesis on southern African alien invasions. There has not been a clear distinction drawn between the effects and mechanics of invasions by aliens and those of native species (e.g. Sculthorpe, 1967; Harper, 1977;

Johnstone, 1986a,b; Ashton & Mitchell, 1989), although some authors do confine themselves to one or the other (e.g. Mack, 1985; Kluge *et al.*, 1986). In Macdonald's opinion, this oversight has important implications as "...any attempt to derive general principles to explain the differential success of invasions which draws examples from both native and alien 'invasions' is almost certainly going to be doomed to failure." (Macdonald, 1991).

Using the example of invasion by woody species into parkland areas of the Kruger National Park, Macdonald (1991) goes on to conclude that the two classes of invasion should be considered separately on the basis that management responses to them are different, and because the forcing functions driving them are different. As the alien is invading purely because it is more competitive than indigenous species in the same area, it can only be controlled by artificially reducing its competitive ability; in Macdonald's example, by directly increasing the mortality of established plants through the use of herbicides. On the other hand, the spread of indigenous species is the result of changes in exogenous disturbances, such as climatic change or atmospheric pollution, or of endogenous disturbances, such as alteration of herbivore-fire-vegetation interactions. This tends to be addressed by community or ecosystem-level manipulation, not by direct remedial management.

The same distinction does not seem to apply to the management of aquatic plant invasions, although in southern Africa there appears to be a tendency to ignore indigenous weed encroachment while alien invasions have received considerable attention. This is illustrated by the relative paucity of information regarding the management of indigenous macrophytes which commonly cause problems, while information regarding the distribution, spread and control of alien aquatic macrophytes is plentiful (e.g. Wild, 1962; Mitchell, 1973, 1977; Jacot Guillarmod, 1979;

Jarvis *et al.*, 1980, 1982; Marshall, 1989). Although indigenous weed species and their control have received considerably more attention internationally (Ashton & Mitchell, 1989), the relative importance of control is heavily weighted toward alien species. The assumption appears to be that the spread of indigenous species can be largely ignored, while aliens always require control.

Perhaps the distinction is drawn because invasions by native species are viewed as part of the process of succession, while invasions by aliens are not. If, however, the relationship between succession and invasion is clearly defined, it becomes clear that the distinction is invalid. Succession, a stochastic process rather than a time-based event, is dependent on three processes of which invasion is just one; the others are maintainance and decline (Johnstone, 1986b). Regardless of where the species originates, the process of invasion is the same and is thus governed by the same principles. This is supported by the fact that the features of successful invaders, and of vulnerable sites, are common both to alien and to native species (Baker, 1964, 1965; Bazzaz, 1984; Arthington & Mitchell, 1986; Newsome & Noble, 1986; Ashton & Mitchell, 1989). Furthermore, alien invaders are intrinsically no more, and no less, successful than native invaders, because the success of invasion by both depends on the removal or overcoming of barriers that previously excluded them from a site. On this basis, there is no reason to distinguish between native and alien invasions in the formulation of invasion theory.

In many cases of encroachment by indigenous species, the fact that a species is a problem is a symptom of inappropriate management practices which inadvertently create "invasion windows" (*sensu* Johnstone, 1986b). These were summarised in Chapter 2 of this thesis. The solution for controlling natives does not lie simply in the removal of the weed, as this does not

eliminate the environmental conditions favouring encroachment and they, or some other species will reappear. Instead, wetlands must be managed in such a way that environmental conditions stress the problem plant, reducing its competitive ability and encouraging reversion to the natural mixed-plant assemblage. Simultaneously, existing stands of the species can be eliminated, or their dominance reduced by applying control measures. Thus, a holistic approach, one including measures to control problem species such as *Typha*, and to reduce its competitiveness, must be adopted.

Management programmes and control measures cannot be separated: once plant stands have been cleared, long-term control is dependent on wetlands being managed so as to reduce the risk of reinvasion and/or overgrowth. While it is both unrealistic and undesirable to eradicate indigenous species, programmes should aim to:

1. remove large-scale infestations which cause management problems;
2. prevent reinvasion of cleared areas, and
3. maintain the remaining stands at an acceptable size.

However, because wetlands serve different purposes from a human perspective and are subject to different environmental conditions, it is important that these objectives are weighted accordingly. This is only possible if the designated role of each wetland is clearly defined, and the most appropriate vegetative assemblage, in terms of species composition, density and distribution, is identified (Chabreck, 1976; Bishop *et al.*, 1979; Tyndall *et al.*, 1982, cited in Johnstone, 1986a). Once the objective is defined, plans to achieve that goal can be made.

In single-purpose wetland systems, it is relatively simple to define management goals, but the process is more complex when considering multi-purpose systems. For example, in Zeekoevlei, rushbeds form an important

waterbird habitat and are cultivated by local residents who use them as windbreaks, and also as a means of providing privacy to their homes (Chapter 3). The vlei is, however, also used for fishing, sailing, rowing and powerboat racing, and sportsmen would rather that all rushbeds were removed. In addition, hydrologists complain that the beds at the inflow to the vlei (Little Lotus River) are restricting flow and are therefore increasing siltation. They, too, would like the rushbeds removed permanently.

For wildlife management, the stands should be maintained in their mature, generative growth phase. To manage the beds for the fishermen, sailors and hydrologists requires their total and permanent removal from at least some parts of the wetland. Thus, effective and sensitive management in this type of wetland is only possible if compromise is reached, and the vlei is zoned, each designated for the different uses. Each area can then be managed with different goals.

Management objectives can be divided into short-term and long-term goals. Short-term goals are aimed at clearing problem areas by utilising control methods that have been shown to remove existing stands (Chapter 6). Long-term goals are the development of wetland management strategies aimed at reducing wetland vulnerability to encroachment. Their objective is to prevent reinvasion and to ensure that remaining populations are maintained at suitable levels, and are confined to acceptable areas.

Management goals are best met if an integrated control programme (ICP) is adopted because no single treatment is suitable for both the removal of problem stands and the maintainance of cleared areas. Although ICPs are complicated to manage, they are more cost-efficient, have fewer adverse impacts on the environment, and are more flexible than single-option programmes (Mitchell, 1986).

## CONTROL

The results of the growth and productivity study (Chapter 4) indicate that efforts to control *Typha* encroachment should concentrate on removing generative stands, because senile stands are already in decline and, without an adequate summer water supply, will be replaced by terrestrial vegetation.

A logical approach to selecting the most effective means of control at each site should start with identifying the methods recommended for the problem plant. These were discussed in Chapter 6, and are summarised in Table 7.1.

The results of local cutting, burning and herbicidal treatment show that total control is most effective if cut shoots are flooded to kill roots, rhizomes and shoot bases, or if stands are subjected to herbicidal treatment. Repeating cutting, burning during dry periods when fires are most intense, and prolonged flooding or wetland drainage also kills stands, but these treatments are more difficult to implement, or take longer to become effective. The choice of control method varies from site to site, depending on the ecosystem under consideration and on the likely impact of plant removal on the environment (Ashton & Mitchell, 1989). When selecting the most appropriate methods the following questions should be considered:

1. Is it physically possible to perform the necessary actions in the area of infestation, and is specialised machinery required?
2. Is it physically safe to use the method in that area? For example, aerial spraying using fixed winged aircraft is not safe if there are power lines or large trees in the vicinity; herbicides should not be used in areas where water is abstracted for domestic or agricultural use, or in residential areas where the chemicals could be inhaled (Ashton

**Table 7.1:** Summary of control methods.

| TREATMENT | ADVANTAGES | DISADVANTAGES |
|---|---|---|
| Manual cutting | - simple<br>- no machinery<br>- no training<br>- harvested material can be utilised<br>- effective if combined with flooding<br>- provides employment | - labour intensive<br>- difficult in deep water |
| Mechanical cutting | - rapid clearing<br>- harvested material can be utilised<br>- effective if combined with flooding | - costly machinery<br>- trained operator |
| Burning | - rapid plant death<br>- cheap | - short term measure<br>- not suitable for all areas<br>- disrupts other aquatic life-forms and ecosystem functioning |
| Herbicides | - effective<br>- cost-efficient | - non-specific<br>- introduces toxic residues into the system<br>- leaves standing litter<br>- need to be reapplied<br>- disrupts other aquatic life-forms and ecosystem functioning |
| Flooding | - effective<br>- cheap<br>- suitable where water levels can be managed | - difficult to implement |
| Draining | - effective if prolonged<br>- suitable where water level can be controlled | - non specific<br>- difficult to implement |

*et al.*, 1979; Steyn *et al.*, 1979).

3. Is the method ecologically sound? For example, is the herbicide under consideration toxic to other aquatic organisms at the concentrations required for control, or will burning large areas of rushbed kill nesting birds?
4. Is the method cost-efficient? Mitchell (1977, 1979) gives simplified methods of analysis designed for macrophyte management.
5. The alternative of doing nothing should be evaluated, considering the greater cost consequences of letting the problem attain its maximum size. This often provides a convincing reason for introducing a control programme which appears too costly either in economic or in environmental terms (Mitchell, 1985).
6. What effect will weed control have on the ecosystem in question? For example:
   - The complete removal, including roots and rhizomes, of *Typha* beds along vlei margins subject to wind induced wave action could increase shoreline erosion (Davies, 1983).
   - The removal of *Typha* stands could create an "invasion window" (*sensu* Johnstone, 1986b) through which other problem plants may become established. Will another plant be more of a problem? Will it be harder to control? Would it be better to eliminate emergent macrophyte habitat altogether, or should *Typha* stands be partially controlled rather than being completely removed from large areas?
   - Large amounts of dead plant material may increase local oxygen demand.
   - The decomposition of litter may release large quantities of plant nutrients (Mitchell, 1986).

Based on the results of this study, the following recommendations are made for the removal and subsequent treatment of *Typha* stands in Cape Flats wetlands. While general guidelines can be given, it is important to note that every aquatic plant problem is unique, and that all local factors must be investigated thoroughly before a particular control programme is chosen (Ashton & Mitchell, 1989). The most appropriate methods should be integrated into a programme that ensures that all life-stages are controlled.

**USE ENVIRONMENTALLY SOUND CONTROL METHODS: CUTTING, BURNING AND HYDROLOGICAL MANIPULATION**

Control methods which mimic natural processes are the most environmentally sound. They are also the most acceptable to the public whose support is necessary for large-scale control (Ashton & Mitchell, 1989). For this reason, cutting or burning *Typha* stands, or manipulating the environment to inhibit plant growth, are recommended for all wetlands.

In the short-term these methods are less cost effective than herbicidal treatment; Ashton, Appleton & Jackson (1986) estimated that manual and mechanical means of control are four times more expensive as chemical control methods, but that chemical control has environmental effects which have not yet been costed. An on-going clearing programme will systematically reduce the extent of the beds if cleared areas are maintained while treating other areas each year, without incurring the risk associated with using herbicides. It will, in addition, create jobs in the economically depressed south-western Cape where there is a large, unskilled work force, and a high level of unemployment. Furthermore, the potential exists to develop industries based on the harvested plant material (Chapter 2).

**Cutting**

*Typha* control is most effective if shoots are cut and the stumps are flooded, using the natural rise in water level to drown the rhizomes. Although research elsewhere has indicated that this should be done during summer, when rhizome stores are lowest, this study has shown that winter cutting and flooding is also effective. In the Cape, with its Mediterranean climate and winter rainfall, winter cutting utilises the natural flood regime and is the only means of flooding rushbeds in vleis where water levels cannot be manipulated artificially.

In systems like Rondevlei where it is not possible to artificially raise water levels, stands should be cut as close to the ground as possible at the start of the winter rains. The subsequent rise in water level will cover shoot stumps, preventing rhizome respiration and causing their death. Any shoots, including dead ones, which protrude above the water at any time during the subsequent four months should be recut to prevent rhizome aeration and shoot regeneration. Seasonal timing is less important than the degree and duration of flooding.

In most wetlands it is unlikely that the entire stand will be flooded during the wet season. In unflooded zones cutting does not prevent shoot regeneration and may enhance emergence, increasing shoot density. Complete control in these areas can only be achieved if regrowth is repeatedly cut (at approximately monthly intervals) until regeneration and recruitment is halted by the exhaustion of rhizome reserves.

**Burning**

During this study "hot" fires (those set in dry areas) eliminated *Typha* by preventing regeneration and recruitment. Fires for controlling the growth of *Typha* should, therefore, be set in summer when there

is maximum drawdown. For reasons of safety they should be confined to relatively small areas and must be carefully controlled. Fire frequency will depend on shoot density. As a rough guide they should be set when standing litter becomes so dense that the stands become difficult to move through. *Typha* stands should be burned only after the breeding season of resident bird species is over.

Winter fires, and those set in flooded areas, did not inhibit shoot emergence and so are not an effective control measure. They did, however, removed standing litter and the driest part (the never-flooded area) of the litter layer thereby reducing total shoot density and enhancing the production of generative shoots. Winter fires are therefore useful for maintaining stands in their generative growth phase (Chapters 4 and 6), thereby increasing the nutritional value of the stand (Thompson & Shay, 1985). Furthermore, there is evidence that regular burning increases habitat diversity by reducing *Typha*'s competitive advantage, and promoting stand invasion by other species (Thompson & Shay, 1989).

Fire is also recommended as a pre-treatment for beds which are going to be cleared by cutting or herbiciding. By reducing shoot density, burning makes subsequent treatment easier and more effective.

**Hydrological manipulation: Flooding or Draining**

The effect of prolonged flooding or draining as means of control were not tested during the course of this study. These methods of environmental manipulation are, however, widely recommended for wetlands where water levels can be controlled (Nelson & Dietz, 1960; Kuflikowski, 1968; van der Valk & Davis, 1979; Farney & Bookhout, 1982; Keddy & Reznicek, 1986; van der Toorn *et al.*, 1990). Furthermore, the responses of *Typha*, in terms of productivity and growth, to flood regime as described in this thesis (Chapter 4) support

the use of hydrological manipulation in the south-western Cape.

*Draining*

In Rondevlei, the driest part of the vlei margins were vegetated by senile stands of *Typha* (Chapter 4). The combination of shading by *Typha* litter and lack of moisture inhibited production of new shoots (Chapter 4), and the sparse stands of live shoots were probably maintained by supplies provided by parts of their genet growing under more favourable conditions (Roberts, 1987). The study showed that *Typha* stands did develop in areas where moisture supplies were marginal, but that these were always sparse stands and showed no signs of spreading into surrounding areas (Chapter 3). Thus, imposing prolonged drawdown conditions would cause the demise of the stands by inhibiting regeneration and causing the death of mature shoots.

Research in other areas of the world indicates that wetlands need to be drained for a minimum of two years for total control of *Typha* (Nelson & Dietz, 1960; van der Toorn *et al.*, 1990). During such events *Typha* shoots die and the area is recolonised by other plants which then prevent the germination of *Typha* seeds. The success of control depends on rapid and prolonged drawdown (Howard-Williams, 1979).

Vleis managed specifically for waterfowl require careful management. These should not be drained when water fowl are nesting or brooding, because drawdown may cause them to abandon their nests (Bedish, 1967). American research has shown that optimal bird habitat comprises a 50:50 ratio of open water to emergent vegetation. This should be created by maintaining open water areas of approximately 0.15ha, set in a matrix of rush beds (Kantrud, 1986; Ball, 1990). Clearings with irregular shapes have the largest circumference and thus provide a larger area of stems

to which invertebrate food species can attach, thereby enhancing secondary production (Danell, 1979).

General drawdown in wetlands that have a uniform basin is unlikely to promote optimal patchy distribution of pools (Ball, 1990), but most marshes have a definite pattern of vegetation and open water which can be re-established when the marshes are reflooded (Bishop *et al.*, 1979). In wetlands without natural open water and vegetated areas, managers can create clearings by removing *Typha* from specified areas, or by deepening pools to make them unsuitable for *Typha* growth (van der Toorn *et al.*, 1990).

Prolonged drawdown is detrimental to wetland bird populations, but this management tool is important for the reestablishment of a mixed plant community (van der Toorn *et al.*, 1990). The long-term effect of stable water levels are just as damaging, as this study (Chapter 2), and others (Weller & Fredrickson, 1974; Bishop *et al.*, 1979) have shown.

The detrimental effects of water-level regulation can be partially negated by stressing *Typha* stands by introducing unpredictable and catastrophic drawdown at irregular (non-seasonal) intervals (Keddy & Reznicek, 1986; Murkin & Ward, 1980). Where water levels fluctuate widely, plant communities develop distinct patterns of vegetative zonation in response to the interactions of stresses imposed on them both by the degree and duration of inundation as well as the degree of exposure (Furness & Breen, 1980; Sousa, 1984), thus favouring a mixed community of short-lived species. Catastrophic drawdown is suitable for use in vleis where the management priority demands reduced seasonal drawdown, because even periodic summer drainage kills, or at least retards, encroachment by existing *Typha* stands.

On the Cape Flats hydrological manipulation has great potential as a cost-efficient means of preventing

encroachment by *Typha* stands. Because many of the wetlands have artificially stabilised flood regimes, their natural flood regime can easily be re-established, reducing the need for further management.

*Flooding*

Areas of the Rondevlei rushbed which were always flooded were colonised by sparse stands of weak *Typha* shoots (Chapter 4). In most cases, these shoots were part of genets from the seasonally-flooded zone which encroached during summer drawdown. The rise in water level during the following winter killed all but the largest shoots, and their growth was inhibited until water levels were once again reduced. The area was only colonised weakly and shoot growth was restricted to periods of low water level. It follows, therefore, that prolonging flooding, at least to winter levels, should both prevent recruitment and kill existing shoots. Beule (1979) has shown that shoots need to be flooded for between two- and thre-years to remove *Typha* stands.

**ONLY USE HERBICIDES AS A LAST RESORT**

Herbicides are cost-efficient in the short term, but need to be reapplied on a regular basis (annually in most cases), reducing their long-term cost effectiveness. Furthermore, the toxic chemicals and their residues threaten wetland ecosystems (Ashton *et al.*, 1979, 1980; Ashton & Mitchell, 1989). While their long-term effects have yet to be established (van der Toorn *et al*, 1990), herbicides have been shown to cause a number of immediate effects, including a reduction in diversity of plant and animal species (Edwards & Davis, 1974; Brooker & Edwards, 1975; Newbold, 1975; Dubey, 1977; Santillo *et al.*, 1989). Under exceptional conditions, herbicides may be necessary to treat very extensive stands that have to be removed quickly. Because of their detrimental

effects on other members of the biota, herbicides should never be used to remove small *Typha* stands which can be easily controlled manually.

When a spraying programme is being planned in the following should be considered:

1. Permission to use herbicides in water bodies must be obtained from the relevant authority. For example, on the Cape Flats, the Director of Nature Conservation should be contacted.
2. Only herbicides registered for use in water bodies should be used. Of the herbicides tested during the course of this study, only Dalapon (trade name Proprop) is registered for the control of *Typha* in South Africa. It is, therefore, illegal to use Glyphosate, a product which is used in Australia and U.S.A.
3. Safe spraying procedures should be followed. For example, in South Africa aerial spraying must comply with the Code of Aerial Application of Agricultural Chemicals of South African Bureau of Standards.
4. If the area to be sprayed lies in a recreational area, the public should be warned that the area is to be treated, and should be kept away during spraying.

**REMOVE PLANT LITTER FROM TREATED AREAS**

Removing litter produced when controlling *Typha* stands, could reduce nutrient loading problems by removing the nutrients locked into plant biomass. As 1ha of dead shoots releases about 180Kg N and 14Kg P in a single pulse (calculated from nitrogen and phosphorus concentrations reported by Boyd, 1970, and Cary & Weerts, 1984) this effect could be significant. In addition, litter decomposes very slowly, especially in unflooded areas (Chapter 5). As a result treated shoots persist as decomposing mounds which are

unsightly and which continue to cause management problems.

It is therefore recommended that litter is removed from treated areas when cut, or as soon after shoot death as possible, unless it is dry enough to burn *in situ*. In order to offset the cost of control, cut shoots can be used for green manure or compost, or even for paper-making (see van Warmelo, 1989 and Chapter 2). Alternatively, litter can be burned except in areas where it could cause a fire hazard.

**LONG-TERM CONTROL REQUIRES A SUSTAINED FOLLOW UP PROGRAMME**

Cleared areas are vulnerable to reinvasion such that the effect of removing *Typha* from large stands will be short-lived unless the area is permanently altered to make it unsuitable for the development of new *Typha* stands. This has a sound theoretical basis: the elimination of the plant from the ecosystem interrupts the successional trend and causes abrupt simplification of the system. The system reverts to an earlier, less stable successional stage which is susceptible to invasion (Ashton & Mitchell, 1989). The follow-up programme should be part of the management strategy adopted for the wetland.

**TREAT PROBLEM AREAS SOONER RATHER THAN LATER**

Leaving a rushbed to develop to its full potential increases the subsequent cost of control as well as the problems caused by the plant stands. Early identification and treatment of potential problem areas is recommended. Wetland managers should be made aware that *Typha*, although indigenous, should be controlled in areas where dense stands are undesirable as soon as shoots appear.

## MANAGEMENT

There is a large body of literature devoted to wetland management and most authors are in agreement on general principles. The underlying assumption is that wetlands are best maintained by leaving them in pristine condition (van der Toorn *et al.*, 1990). Such a strategy is, however, unrealistic for wetlands in urban and perturbated catchments. Ways must be found to reduce the impact of development management on natural wetland functions, thus retaining their benefits and values.

The first step toward successful management is to decide what the wetland is to be managed for. Management goals for single purpose systems are usually clear. For example, Rondevlei is a Bird Sanctuary and management goals include providing a variety of natural habitat to encourage bird species diversity, while the primary purpose of another wetland may be for wastewater treatment, and the primary management goal would be the establishment of macrophyte stands which improve water quality. Most wetlands have, however, more than one use and management subsequently becomes more complicated. Multiple use has the advantage that systems treated holistically generally remain more balanced than those in which management has a single objective (van der Toorn *et al.*, 1990).

Management programmes should be directed toward long-term goals and adapted to local situations. For this objective to be met it is important that wetland managers understand how the wetlands they manage function (Straskraba, 1990), and that they are aware of the major factors affecting plant growth and species diversity. In most wetlands these are water level, salinity and nutrient level (Bishop *et al.*, 1979; Weller, 1975, 1978; Chabreck, 1976; Howard-Williams, 1979; Keddy & Reznicek, 1986; Axelson & Julian, 1988; Breen *et al.*, 1988; van der Toorn *et*

*al.*, 1990). Finally, when dealing with specific plants detailed knowledge of the effects of environmental conditions on life-history, growth and productivity is necessary before it is possible to develop appropriate management techniques for enhancing, or preventing, growth.

The implementation of management programmes should be accompanied by detailed documentation of procedures and results. Records of what occurred before and after specific procedures were implemented serve as useful guides to what can be expected if similar techniques are used elsewhere, and can be used to great effect as a public relations tool (van der Toorn *et al.*, 1990). By being able to predict the results and to monitor changes, it is possible to provide reassurance and to gain support from the public, even for apparently "drastic" procedures.

Regular aerial photographs of the treated area are a useful tool for recording results, but if they are used to monitor changes in vegetation structure it is important that they are taken at a definition suitable for vegetation mapping (at least 1:50 000 scale; Weisser & Stadler, 1983).

A useful example of the value of recording the results in the implementation of a management programme is the study of the relationship between management strategy and aquatic macrophyte communities in the Somerset Levels, UK (Wolseley, 1986). The results clearly showed the changes following any given management procedure (Table 7.2), and they have been used to formulate management programmes aimed at optimising species diversity and wetland stability in various parts of the UK. For example, a two- to five-year clearing cycle promotes species and habitat diversity with low monocot cover if management conditions remain stable (i.e. no eutrophication or changes to hydrology). Other examples of this type of study include those of Goldsborough & Robinson (1986),

**Table 7.2:** Example of the effects of different management procedures on the vegetation structure of Somerset ditches and dykes (after Wolseley, 1986).

| MANAGEMENT | RESULT |
|---|---|
| Nutrient enrichment | Increased cover, decreased species diversity |
| Increased flow | Decreased surface cover, increased number of submerged species |
| Increased salinity | Increased *Potamogeton pectinatus*, and later, *Phragmites* spp. |
| No active management for 7 years: | |
| non-arable area | Increased bank shading resulting in growth of macrophytes becoming lank |
| arable area | Decreased diversity; increased monocot cover |
| grazed area | Decreased diversity; increased numbers of small emergent species |
| Dredging | Decreased species diversity |
| Annual clearing: | |
| by hand | Increased submergent species cover |
| mechanical | Decreased submergent and emergent species cover. Scraping decreased species diversity as monocots became dominant; cutting increased species diversity, especially among dicots |

Murphy *et al.* (1987) and Gryseels (1989).

Mitchell (1986) emphasises the importance of systematically recording the results of weed control procedures, saying that they provide a means of understanding wetland resilience and the assimilative capacity of wetlands toward weed management stategies. In his opinion, the absence of a theoretical understanding of this aspect of weed management is the major gap in our understanding of aquatic weed science.

## SPECIFIC MANAGEMENT RECOMMENDATIONS FOR THE CAPE FLATS.

### Introduction

Encroachment and the development of monospecific *Typha* stands can be reduced by creating an environment in which *Typha* growth is stressed. This study, and those performed in other parts of the world, have shown that the creation of germination sites, the stabilisation of flood regimes and eutrophication are three factors which promote invasion and encroachment. Their elimination should therefore inhibit these processes.

*Creation of Germination Sites*

Gradual drawdown, bank clearing and siltation create unshaded damp sand banks which are suitable for the germination of *Typha* seeds, making the banks vulnerable to invasion (Chapter 4). Where water levels have been stabilised, seedlings have a much greater chance of becoming established because water-level regulation prevents them from being inundated until they are large enough to withstand the inhibitory effects of prolonged flooding (Chapter 4).

*Stabilisation of Natural Flood Regimes*

Natural selection under stable hydrological regimes favours large plants that are able to conserve nutrients and resources, and which possess specialised adaptations to cope with anoxic soil conditions (Breen *et al.*, 1988). Their competitive growth form then prevents the growth of competing species, and a monospecific stand develops.

Relatively stable water levels are a feature of all wetlands on the Cape Flats which have a "*Typha* problem", while the species is generally absent from those subject to large seasonal fluctuations in water depth and to bank inundation (Chapter 3). Historical records show that *Typha* was generally absent from wetlands prior to the stabilisation of water levels, but invaded them soon after regulation was instituted (e.g. Rondevlei, Middlemiss, 1974). A similar situation has been reported from Iowa (Bishop *et al.*, 1979), Manitoba (Murkin & Ward, 1980) and California (Beare & Jedler, 1987)

Results presented in Chapter 4 support observations that water level stability is implicated in encroachment, showing that expansion of *Typha* stands is largely governed by the availability of water during the summer growth period. Summer drawdown, the normal situation in south-western Cape wetlands, inhibits encroachment because growth is retarded by dry conditions along the upper edges of vlei margins. Where growth is not inhibited by lack of water during summer, annual production is significantly higher and stands are larger, denser and more productive (Chapter 4). High shoot densities and increased litter production (Chapter 4) appear to enhance the rate of hydrosere succession, promoting encroachment into areas where growth was previously limited by water depth.

*Eutrophication*

Although direct evidence linking encroachment to eutrophic habitats is not presented in this thesis, the relationship has been demonstrated in Australia (Aston, 1973, cited in Ashton & Mitchell, 1989). High concentrations of plant nutrients enhance encroachment because stands are more productive (Dykyjova, 1978; Thompson, 1985). In fact, *Typha* is most competitive under eutrophic conditions, being replaced when nutrients become limiting (Szczepanska & Szczepanska, 1976). Catchment management programmes which include provision for controlling the levels of eutrophication thus have the potential to reduce encroachment, even if sites that are physically vulnerable to invasion exist.

**Recommendations**

Management programmes should therefore take cognisance of the following to prevent *Typha* encroachment:

**1. Do not reduce summer drawdown**

It is clear that the "*Typha* problem" in Cape Flats wetlands would largely be solved if their natural flood regimes were reestablished. Where possible, existing water regulating constructions should be removed, and they should not be built in vleis which have the morphometric and nutrient potential to support large stands of emergent vegetation. If some degree of regulation is absolutely necessary, sluice gates should be installed as they can be used to alter water levels with a minimum of expense. These structures could also be introduced into existing weirs.

**2. Reduce the availability of germination sites**

*Typha* seeds germinate most successfully on unshaded damp sand or mud flats. As these environments are important waterfowl habitats it is unreasonable to expect that they can be eliminated from wetlands vulnerable to *Typha* encroachment. Nevertheless, it is possible to reduce the chances of invasion by ensuring that seedlings do not become established, either by subjecting them to flooding or to drought conditions, or by manually removing them.

The Cape vlei survey (Chapter 2) showed that margins dredged to create a steep shelf at least 1.0m deep eliminated the shallow banks on which seedlings germinate. While the damage caused by dredging to wetland ecosystems is recognised, this method of removing germination sites may be useful where bulrush growth is least desirable, such as around slipways or in fishing areas.

*Typha* stands blocking canals can be eliminated by ensuring that canal floors are maintained to prevent cracking, and to reduce the build up of a sand layer in which seedlings can germinate. Canals do not provide suitable habitats for aquatic organisms and therefore tend to act merely as

conduits for water rather than supporting functional aquatic ecosystems. Both canals and dredging are used to treat problems created by man in the first place, and the long-term solution probably lies in trying to bring systems back into their natural state of equilibrium. To this end, there is pressure on those responsible for river management to break up existing canal structures, creating riparian wetlands. The development of the wetlands will require careful monitoring, and if necessary, further, sensitive management, to prevent the development of undesirable monospecific rush- or reedbeds.

**CONCLUDING REMARKS**

The evidence presented in this thesis shows that *Typha* is spreading between and around the wetlands of the south-western Cape. It is also clear that the "problem" is caused by inadequate wetland management, rather than by exogenous factors. By treating the problem in a sensitive and innovative manner it should be possible to solve it, and to use it to create opportunities for the local residents, thereby encouraging them to become involved in the conservation and effective management of the Cape Flats wetlands.

In southern and central Africa, the protectionist policies usually adopted towards wildlife and ecosystem conservation are being replaced by community-based methods which are founded on the principle of sustainable utilisation (Butchart, 1992). Examples of the successful implementation of these ideals include the CAMPFIRE scheme in Zimbabwe, the NPWS/ADMADE programme in Zambia and the recent creation of the Richtersveld National Park in South Africa. The rationale behind these programmes is that it is essential for the people directly affected by conservation efforts to benefit from them in a material way, thereby assisting in conservation efforts by direct involvement. The most simple example is that starving and impoverished people living around a wildlife sanctuary are unlikely to refrain from killing animals for food unless the creation of the sanctuary provides them with an

alternative means of survival. It is only when the community becomes involved, and is shown the benefits of conservation, that they perceive the true long-term value of the ecosystems around them (Butchart, 1992).

These principles can be applied to urban wetland conservation too. Many of the wetlands of the Cape Flats are situated in high-density suburbs where there is large-scale overcrowding, unemployment and poverty. Under these conditions, wetland conservation has no meaning, and receives little attention from residents. Householders in the vicinity of wetlands perceive them as wastelands to be used as dumping areas, as a menace to children and to animals who have been known to drown after falling through the litter mat, and as overgrown areas which harbour vagrants who are considered a criminal threat. If, however, residents are shown that wetlands can be utilised both for job creation and as a source of recreation, the community might begin to perceive them as resources worth caring for. Clearing the stands of *Typha* would immediately improve the wetlands' physical appearance, enhancing their role as recreational areas, reducing littering and preventing their use by vagrants. In the long-term, if wetlands are valued, the community will support efforts to preserve wetlands as part of the urban green belts, improving the appearance and health of the region. On a larger scale, the creation of conservation areas in the townships will provide a means of putting the people "back in touch" with the natural environment, and introducing a means of educating the community about environmental concerns. This is a vital long-term goal, for "... the establishment of a nation-wide programme of environmental literacy is crucial to the very survival of South Africa in the future." (Farienda Kahn, in Holt-Biddle, 1992).

To this end, it is strongly recommended that control of *Typha* is instituted by manual cutting followed by flooding. By rejecting mechanisation as a means of clearing the wetlands it is possible to create more jobs, and these will be available to unskilled workers. Utilising the the harvested material would offset some of the costs of

control and would provide either litter with which to make compost, improving the condition of the poor soils found on the Cape Flats, or material for hand crafts such as basket weaving. The cut-and-flood combination of treatments is effective and utilises the wetlands' natural flood regime, eliminating the need for artificial flooding thereby incurring less expense.

Herbicides should not be used as their long-term effect on wetland ecosystem functioning is likely to be harmful. Furthermore, the use of sophisticated, expensive, labour-saving "First-World" technology in a "Third-World" environment is unjustified when there is labour available, and the opportunity exists to create employment opportunities. Finally, reducing the use of toxic chemicals in delicate ecosystems such as wetlands is a highly desirable goal, eliminating environmental contamination and the risk imposed by the chemicals on the communities living near the affected areas.

**REFERENCES**

ARTHINGTON, A.H. and MITCHELL, D.S. 1986. Aquatic invading species. In: *Ecology of Biological Invasions: An Australian Perspective*. Groves, R.H. and Burdon, J.J. (eds). Australian Academy of Science, Canberra.

ASHTON, P.J., APPLETON, C.C. & JACKSON, P.B.N. 1986. Ecological impacts and economic consequences of alien invasive organisms in southern African aquatic ecosystems. In: *The Ecology and Management of Biological Invasions in Southern Africa*. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A. (eds). Oxford University Press, Cape Town.

ASHTON, P.J. & MITCHELL, D.S. 1989. Aquatic plants: Patterns and modes of invasion, attributes of invading species and assessment of control programmes. In: *Biological Invasions: A global perspective*. Drake, J.A., Mooney, H.A., diCastri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. & Williamson, M. (eds). Wiley Press, New York.

ASHTON, P.J., SCOTT, W.E. & STEYN, D.J. 1980. The chemical control of the water hyacinth (*Eichhornia crassipes* (Mart.) Solms). *Progress in Water Technology*, **12**: 865-882.

ASHTON, P.J., SCOTT, W.E., STEYN, D.J. & WELLS, R.J. 1979. The chemical control programme against the water hyacinth *Eichhornia crassipes* (Mart.) Solms on Hartbeespoort Dam: Historical and practical aspects. *S.A. J. Sci.*, **75**: 303-306.

AXELSON, S. & JULIAN, C. 1988. Weed control in small dams. Part 1. Introduction: Control of algae and of cumbungi. *Queensland Agric. J.*, **July-Aug**: 241-246.

BAKER, H.G. 1964. Patterns of plant invasions in North America. In: *Ecology of Plant Invasions in North America and Hawaii*. Mooney, H.A. & Drake, J.A. (eds). Springer-Verlag, Berlin.

BAKER, H.G. 1965. Characteristics and modes of origin of weeds. In: *The Genetics of Colonising Species*. Baker, H.G. & Stebbins, G.L. (eds). Academic Press, London.

BALL, J.P. 1990. Influence of subsequent flooding depth on cattail control by burning and mowing. *J. Aquat. Plant Mngmt.*, **28**: 32-36.

BAZZAZ, F.A. 1984. Demographic consequences of plant physiological traits: Some case studies. In: *Perspectives in Plant Population Ecology*. Dirzo, R. & Sarakan, J. (eds). Sinauer Associates Inc., Sunderland.

BEARE, P.A. & JEDLER, J.B. 1987. Cattail invasion and persistence in a coastal salt marsh - the role of salinity intrusion. *Estuaries*, **10**: 165-170.

BEDISH, J.W. 1967. Cattail moisture requirements and their significance to marsh management. *Am. Midl. Nat.*, **78**: 288-300.

BEULE, J.D. 1979. *Control and management of cattails in south eastern Wisconsin wetlands*. Tech. Bull. No. 112. Dept. Nat. Res., Madison, Wisconsin.

BISHOP, R.A., ANDREWS, R.D. & BRIDGES, R.J. 1979. Marsh management and its relation to vegetation, waterfowl and muskrats. *Proc. Iowa Acad. Sci.*, **86**: 50-56.

BOYD, C.E. 1970. Vascular aquatic plants for mineral nutrient removal from polluted waters. *Econ. Bot.*, **24**: 95-103.

BREEN, C.M., ROGERS, K.H. & ASHTON, P.J. 1988. Vegetation processes in swamps and flooded plains. In: *Vegetation of inland waters*. Symoens, J.J. (ed.). Kluwer Academic Publishers, London.

BROOKER, M.P. & EDWARDS, R.W. 1975. Aquatic herbicides and the control of water weeds. *Wat. Res.*, **9**: 1-15.

BUTCHARD, D. 1992. South Central Africa. The Bushcall Environmental Review 1991. *Bushcall Annual*, **1992**: 7-20.

CARY, P.R. & WEERTS, P.G.J. 1984. Growth and nutrient composition of *Typha orientalis* as affected by water temperature and nitrogen and phosphorus supply. *Aquat. Bot.*, **19**: 105-118.

CHABRECK, R.H. 1976. Mangement of wetlands for wildlife habitat improvement. In: *Estuarine Processes: 1. Uses, stresses and adaption to the estuary*. Wiley, M. (ed.). Academic Press, London.

DANELL, K. 1979. Reduction of aquatic vegetation following the colonisation of a northern Swedish lake by the muskrat Ondatra zibethica. *Oecol. (Berl.)*, **38**: 101-106.

DAVIES, B.R. 1983. *Report on reed removal at Zeekoevlei and commentary on aerial photographs (1968 and 1980) showing the development of emergent and submerged vegetation in the vlei*. Unpublished report No.6. Cape Town City Council, Cape Town.

DUBEY, P.S. 1977. Herbicidal pollution - pollen damage due to herbicides. *Environ. Poll.*, **3**: 169-172.

DYKYJOVA, D. 1978. Nutrient uptake by littoral communities of helophytes. In: *Pond Littoral Ecosystems: Structure and Functioning*. Dykyjova, D. & Kvet, J. (eds). Ecological Studies, **28**. Springer-Verlag, Berlin.

EDWARDS, A.C. & DAVIS, D.E. 1974. Effects of herbicides on *Spartina* salt marsh. In: *Ecology of Helophytes*. Reimold, R.J. & Queen, W.H. (eds). Academic Press, London.

FARNEY, R.A. & BOOKHOUT, T.A. 1982. Vegetation changes in a Lake Erie marsh (Winous Point, Pttawa Country, Ohio) during high water years. *Ohio J. Sci.*, 82: 102-107.

FURNESS, H.D. & BREEN, C.M. 1980. The vegetation of seasonal flooded areas of the Pongolo River floodplain. *Bothalia*, **13**: 217-231.

GOLDSBOROUGH, L.G. & ROBINSON, G.G.C. 1980. Changes in periphytic algal community structure as a consequence of short herbicide exposures. *Hydrobiologia*, **139**: 177-192.

GRYSEELS, M. 1989. Nature management experiments in a derelict reedmarsh. 1. Effect of winter cutting. *Biol. Cons.*, **47**: 171-193.

HARPER, J.L. 1977. *Population Biology of Plants*. Academic Press, London.

HOLT-BIDDLE, D. 1992. The Bushcall Forum. *Bushcall Annual*, **1992**: 49-62.

HOWARD-WILLIAMS, C. 1979. The distribution of aquatic macrophytes in Lake Chilwa: Annual and long-term fluctuations. In: *Lake Chilwa: Studies of change in a tropical ecosystem*. Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds). Dr W. Junk Publishers, The Hague.

JACOT GUILLARMOD, A. 1979. Water weeds in southern Africa. *Aquat. Bot.*, **6**: 377-391.

JARVIS, M.J.F., MITCHELL, D.S. & THORNTON, J.A. 1980. Aquatic macrophytes and *Eichhornia crassipes*. In: *Limnology of some selected South African Impoundments*. Walmsley, R.D. & Butty, M. (eds). Water Research Commission, Pretoria.

JARVIS, M.J.F., MITCHELL, D.S. & THORNTON, J.A. 1982. Aquatic macrophytes and *Eichhornia crassipes*. In: *Lake McIlwaine: The eutrophication and recovery of a tropical man-made lake*. Thornton, J.A. & Nduku, W.K. (ed.). Dr W. Junk Publishers, The Hague.

JOHNSTONE, I.M. 1986a. Macrophyte management: An integrated perspective. *N.Z. J. Mar. Freshwater Res.*, **20**: 599-614.

JOHNSTONE, I.M. 1986b. Plant invasion windows: A time-based classification of invasion potential. *Biol. Rev.*, **61**: 369-394.

KANTRUD, H.A. 1986. *Effects of vegetation manipulation on breeding waterfowl in Prairie wetland - a literature review*. Fish and Wildlife Technical Report 3. Washington D.C.

KEDDY, P.A. & REZNICEK, A.A. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *J. Great Lakes Res.*, **12**: 25-36.

KLUGE, R.L., ZIMMERMANN, H.G., CILLIERS, C.J. & HARDING, G.B. 1986. Integrated control for alien weeds. In: *The Ecology and Management of Biological Invasions in southern Africa*. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A. (eds). Oxford University Press, Cape Town.

KUFLIKOWSKI, T. Vegetation of the Doczalkowice Dam reservoir in the years 1964-1966. *Acta Hydrobiol.*, 10: 163-178.

MACK, R.N. 1985. Invading plants: Their potential contribution to population biology. In: *Studies on Plant Demography*. White, J. (ed.). Academic Press, London.

MACDONALD, I.A.W. 1991. *Conservation implications of the invasion of southern Africa by alien organisms*. PhD Thesis, Department of Zoology, University of Cape Town, Cape Town.

MARSHALL, B.E. 1989. The water hyacinth problem in Lake McIlwaine. *Zim. Sci. News*, **23**: 91-94.

MARTIN, A.R.H. 1968. Pollen anaysis of Groenvlei Lake sediments, Knysna (South Africa). *Rev. Palaeobotan. Palynol.*, 7: 107-144.

MIDDLEMISS, E. 1974. *The Rondevlei Bird Sanctuary. A record of the environment, 1952-1974*. Divisional Council of the Cape, Cape Town.

MITCHELL, D.S. 1973. Aquatic weeds in man-made lakes. In: *Manmade Lakes: Their Problems and Environmental Effects*. Ackermann, W.C., White, G.F. & Worthington, E.B. (eds). American Geophysical Union, Washington.

MITCHELL, D.S. 1977. Water weed problems in irrigation systems. In: *Arid Land Irrigation in Developing Countries*. Worthington, E.B. (ed.). Pergamon Press, Oxford.

MITCHELL, D.S. 1979. Formulating aquatic weed management programmes. *J. Aquat. Plant Mngmt.*, **17**: 22-24.

MITCHELL, D.S. 1985. African aquatic weeds and their management. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, Dordrecht.

MITCHELL, D.S. 1986. The impacts of aquatic weed control on aquatic ecosystems. *Proceedings of the European Weed Research Society 7th Symposium on Aquatic Weeds*, Loughborough, England.

MURKIN, H.R. & WARD, P. 1980. Early spring cutting to control cattail in a northern marsh. *Wildl. Soc. Bull.*, **8**: 254-256.

MURPHY, K.J., FOX, A.M. & HANBURY, R.G. 1987. A multivariate assessment of plant management impacts on macrophyte communities in a Scottish canal. *J. Appl. Ecol.*, **24**: 1063-1079.

NELSON, N.F. & DIETZ, R.H. 1960. *Cattail control methods in Utah*. Utah State Department of Fish and Game Publication No. 66-2.

NEWBOLD, C. 1975. Herbicides in aquatic systems. *Biol. Cons.*, **7**: 97-118.

NEWSOME, A.E. & NOBLE, I.R. 1986. Ecological and physiological characters of invading species. In: *Ecology of Biological Invasions*. Groves, R.H. & Burdon, J.J. (eds). Cambridge University Press, Cambridge.

ROBERTS, J. 1987. *The Autocology of Typha spp. in South-Eastern Australia*. PhD THesis, University of Adelaide, Australia.

SANTILLO, D.J., BROWN, P.W. & LESLIE, D.M. 1989. Response of song birds to glyphosate-induced habitat changes on clearcuts. *J. Wildl. Mngmt.*, **53**: 64-71.

SCOTT, L. & BONNEFILLE, R. 1986. Search for pollen from hominid deposits of Kromdraai, Sterhfontein and Swartkrans: some problems and preliminary results. *S. Afr. J. Sci.*, 82: 380-382.

SCULTHORPE, C.D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold Publishers, London.

SOUSA, W.P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. System.*, **15**: 353-391.

STEYN, D.J., SCOTT, W.E., ASHTON, P.J. & VIVIERS, F.S. 1979. *Guide to the use of herbicides on aquatic plants*. Unpublished report, Pretoria.

STRASKRABA, M. 1990. Shallow lakes and reservoirs. In: *Wetlands and Shallow Continental Water Bodies*. Pattern, B.C., Jorgenson, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

SZCZEPANSKA, W. & SZCZEPANSKA, A. 1976. Growth of *Phragmites communis* Trin., *Typha latifolia* L. and *Typha angustifolia* L. in relation to the fertility of the soils. *Pol. Arch. Hydrobiol.*, **23**: 233-248.

THOMPSON, D.J. & SHAY, J.M. 1985. The effects of fire on *Phragmites australis* in the Delta marsh, Manitoba. *Can. J. Bot.*, **63**: 1864-1869.

THOMPSON, D.J. & SHAY, J.M. 1989. First-year response of a *Phragmites* marsh community to seasonal burning. *Can. J. Bot.*, **67**: 1448-1455.

THOMPSON, K. 1985. Emergent plants of permanent and seasonally flooded wetlands. In: *The Ecology and Management of African Wetland Vegetation*. Denny, P. (ed.). Dr W. Junk Publishers, Dordrecht.

VAN DER TOORN, J., VERHOEVEN,,J.T.A.A. & SIMPSON, R.L. 1990. Freshwater marshes. In: *Wetlands and Shallow Water Continental Water Bodies*. Pattern, B.C., Jorgensen, S.E. & Dumont, H. (eds). SPB Academic Publishing, The Hague.

VAN DER VALK, A.G. & DAVIS, C.B. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. *Aquatic Botany*, 6: 29-51.

VAN WARMELO, W. (ed.). 1989. *Typha: Its status, problems, economic benefits and control*. Report on Symposium held in Cape Town, 9 March, 1989. Botanical Society of South Africa, Cape Town.

WEISSER, P.J. & STADLER, A. 1983. Suitability of aerial photographs for monitoring emergent and submerged macrophyte vegetation in the Wilderness Lakes, S. Africa. *Proceedings of the International Symposium on Aquatic Macrophytes*, Nijmegen.

WELLER, M.W. 1975. Studies of cattail in relation to management for marsh wildlife. *Iowa State J. Res.*, **49**: 383-412.

WELLER, M.W. 1978. Management of freshwater marshes for wildlife. In: *Freshwater Wetlands*. Good, R.E., Whigham, D.F. & Simpson, R.L. (eds). Academic Press, New York.

WELLER, M.W. & FREDERICKSON, L.H. 1974. Avian ecology of a managed glacial march. *Living Bird*, 12: 269-291.

WILD, H. 1962. Harmful aquatic plants in Africa and Madagascar. *Kirkia*, 2: 1-66.

WOLSELEY, 1986. The aquatic macrophyte communities of the ditches and dykes of the Somerset Levels and their relation to management. *Proceedings of the European Weed Research Society 7th Symposium on Aquatic Weeds*, Loughborough, England.